06.1
A5
Arn

NOV 5 1918

GENERAL LIBRARY
NOV 7 1918
UNIV. OF MICH.

54—2

Proceedings of the American Academy of Arts and Sciences

Vol. 54. No. 2.— September, 1918.

SIZE VARIATION IN TRACHEARY CELLS:

I. A COMPARISON BETWEEN THE SECONDARY XYLEMS OF VASCULAR CRYPTOGAMS, GYMNOSPERMS AND ANGIOSPERMS.

By I. W. Bailey and W. W. Tupper.

(Continued from page 3 of cover.)

VOLUME 54.

1. FOYE, WILBUR GARLAND.— Geological Observations in Fiji. pp. 1–145. 1 pl. September, 1918. $2.00.
2. BAILEY I. W., AND TUPPER, W. W.— Size Variation in Tracheary Cells: I. A Comparison between the secondary Xylems of vascular Cryptogams, Gymnosperms and Angiosperms. pp. 147–204. September, 1918. 75c.

Proceedings of the American Academy of Arts and Sciences.

Vol. 54. No. 2.—September, 1918.

SIZE VARIATION IN TRACHEARY CELLS:

I. A COMPARISON BETWEEN THE SECONDARY XYLEMS OF VASCULAR CRYPTOGAMS, GYMNOSPERMS AND ANGIOSPERMS.

By I. W. Bailey and W. W. Tupper.

SIZE VARIATION IN TRACHEARY CELLS:

I. A COMPARISON BETWEEN THE SECONDARY XYLEMS OF VASCULAR CRYPTOGAMS, GYMNOSPERMS AND ANGIOSPERMS.[1]

By I. W. Bailey and W. W. Tupper.

Received, February 10, 1918.

Introduction.

In the study of cell size in plants and animals, much emphasis is placed, during the last thirty years, upon the relations between cell size and body size, organ size and nuclear size. Sachs (1893) calls attention to the fact that, although plants and animals vary enormously (0.001 mm. to 100 m.) in their linear dimensions, there is not a proportional variation (0.001 to 0.05 mm.) in the size of their cells. He formulates (p. 73) the generalization that "zwischen der Grösse der Organe und der ihrer Zellen keinerlei Proportionalität besteht; die Grösse der Organe, zumal homologer Organe, steht vielmehr mit der Zahl der Zellen im Verhältniss." His assistant Amelung (1893) reaches a similar conclusion (p. 187): "Dass nämlich bei morphologisch gleichen Pflanzentheilen trotz der ausserordentlichen Grössenunterschiede doch die mittleren Zellengrössen dieselben bleiben." Strasburger (1893) emphasizes the fact that, although individuals of the same species always show the same size of embryonic nuclei and cells, regardless of variations in the size of their growing points, varieties of these same species may differ greatly from each other.

The conclusions of Sachs and Amelung, in regard to the "fixed size of specific organ-cells," are supported by those of a number of other investigators. For example, Conklin (1896) finds that, in dwarfs of *Crepidula plana*, the cells are of approximately the same size as in normal forms, and (1898) that sexually dimorphic individuals of this species, although differing greatly in body size, are composed of cells of similar sizes. Rabl (1899) considers that the cells of the crystalline lens vary appreciably in number, but not in size. The work of Driesch (1898 & 1900) is particularly suggestive. He shows that in

[1] This paper was presented in preliminary form at the Columbus meeting of the American Association, December, 1915.

"partial" larvae, derived from isolated blastomeres or egg fragments, and in "double" larvae, from fused eggs, body size is directly proportional to the number of constituent cells. As a result of these observations upon echinids, he concludes (1900, p. 384) that, "die Zellengrösse der zellen einzelner specifischer Organe scheint eine so fest fixirte Grösse zu sein, wie es die optischen Richtungen am Krystall sind." Schnegg (1902), in studying the genus Gunnera, records a number of measurements which corroborate the work of Amelung. Boveri (1904) shows that the epithelial cells, from tongues of dwarfs and giants of the human species, are of the same size as those from individuals of normal stature, and Schultz (1904) states (p. 559): "so will ich für die Planarien wenigstens das Gesetz aufstellen, dass bei Verkleinerung der Form infolge von Inanition die Zellen nicht an Grösse, sondern nur an Zahl abnehmen — und zwar in allen Organen Proportional den Grössen verhältnissen dieser Organe zueinander." Ewart (1906) concludes that, in unusually large leaves, formed upon defoliated trees, there is an increase in the number, but not the size of the cells. [2]

Very different results are secured, however, by another group of investigators. From his study of the spinal cord of the frog, Gaule (1889) is led to place much emphasis upon the constancy of cell number. Donaldson (1895) similarly concludes (p. 162) that "the determination of the number of neuroblasts occurs so early in the history of the individual, and under such uniform conditions, that it is very difficult to regard the environment as possessed of much power to cause variation in this respect." He considers that differences in the weight of the human brain are due mainly to differences in the size of the nerve cells. Hardesty (1902), who made a comparative study of the spinal cords of various mammals, finds that the motor nerve cells are largest in the elephant and smallest in the mouse.

In view of the importance attached to the "Kernplasmarelation" by Gerassimow (1902), Boveri (1905), Hertwig (1903) and others, Gates' (1909) observations upon cell size in *Oenothera gigas*, a tetraploid mutation of *Oe. Lamarkiana*, are of considerable interest. He states (p. 543): "In *O. gigas* we have an organism built of bricks which are larger and whose relative dimensions are also altered in some cases. These two factors will apparently account for all the differences between *O. gigas* and *O. Lamarkiana*, and the second factor may be one

2 More recently, Tenopyr (1918) endeavors to prove that differences in the shape of leaves are dependent upon variations in the number rather than the shape of their constituent cells.

merely of readjustment consequent upon the first. It is probable that the number of cells is approximately the same in both cases." Similar phenomena are recorded by Winkler (1916) and Tupper and Bartlett (1916 & 1918). The work of Gregory (1911) and Keeble (1912), on the other hand, indicates that in giant forms of *Primula sinensis*, which have larger cells than normal, there is an increase in the size, but not in the number of chromosomes.

Morgan (1904) and Chambers (1908) find that the eggs laid by a given individual may vary greatly in size, and the latter investigator, who questions the doctrine of the fixity of cell size, considers that body size and cell size are proportional to the size of the eggs from which the animals are formed. Popoff (1908) also supposes that body size is determined by the size of the reproductive cells, but Conklin (1912a), as a result of his later investigations upon Crepidula, concludes (p. 186): "In the different species of this genus the size of the germ cells does not determine the size of the adult (Popoff, Chambers). Within the same species differences in body size are due in the main to differences in cell number, the cell size being approximately constant."

It is to be noted, in passing, that in many of these investigations which tend to emphasize the constancy of cell size or cell number in specific animals or plants, scant attention is given to the work of botanists[3] and zoölogists who concern themselves with the study of variations due to environmental factors. Heumann (1850), Morpurgo (1888 and 1889), Frank (1895), Gauchery (1899), Lippold (1904), Stoppenbrink (1905) and Morgulis (1911) describe a number of dwarfs or depauperate plants or animals which are composed of smaller tissue-cells than normal individuals or giants. However, it is noted, particularly by Morpurgo, Gauchery and Morgulis that different categories of tissues may behave very differently during inanition. Kraus (1869–70) emphasizes the fact that the cells of the long internodes of etiolated plants are longer than those of plants grown under normal illumination, and MacCallum (1898) calls attention to the fact that the increase in the musculature of an adult and muscular hypertrophy may be due to an increase, not in the number, but the size of the muscle fibers.

The investigations of Sanio (1872), Haberlandt (1882), Illing (1905),

3 The works of Areschong, Brenner, Bonnier, Costantin, Derschau, Dassonville, Dufour, Eberdt, Eberhardt, Frank, Géneau de Lamarlière, Grosglik, Haberlandt, Hesselman, Johow, Kohl, Lesage, Mer, Nordhausen, Pick, Sauvageau, Schuster, Stahl, Tschirch, Vesque, Volkens, Weiss, Zinger and many others, who studied the effects of light, temperature, moisture, nutrition, etc. upon the form and structure of plants, contain numerous incidental references to variations in cell size, but unfortunately few exact measurements.

Berezowski (1910), Yapp (1912), Schramm (1912) and Paulmann (1915) are particularly significant, since they show very clearly that the size of the cells of a given tissue may vary considerably in different parts of an organ or individual and during different stages in its growth or ontogeny.

Hertwig (1903) notes the importance of the fact that the "Kernplasmarelation" is subject to considerable variation during the life of a cell and, therefore, determines this ratio during a particular phase in the development of cells. The results of Conklin's (1912) work upon *Crepidula plana* are of interest in this connection. He states (p. 25): "The results of my measurements do not indicate that the Kernplasma-Relation of Hertwig is either a constant or self regulating ratio in the blastomeres of these eggs; on the other hand it appears to be a result rather than a cause of the rate of cell division, and consequently it is a variable rather than a constant factor. Furthermore, the size of the nucleus, in these eggs, is dependent upon at least three factors: (1) The initial quantity of chromatin (number of chromosomes) which enter into the formation of the nucleus (Boveri). (2) The volume of the protoplasm in which the nucleus lies. (3) The length of the resting period."

The necessity of distinguishing between purely somatic variations in cell size and those that are truly germinal, is fully appreciated by Jennings (1908), in his careful work upon unicellular organisms. On the botanical side, Zalenski (1904), Kolkunow (1905, 1907, 1907a and 1913) and Jakushkine and Wawilow (1912), in a series of important papers published unfortunately in Russian, show that, although the size of the stomata and guard cells vary considerably in different parts of an individual and under different environmental conditions, there is an inherited norm which varies in different races or varieties of our commonly cultivated cereals. They find that certain of the larger races possess larger stomata, but this is not true in all cases. In his study of nanism, Sierp (1914) emphasizes the necessity of differentiating between true constitutional dwarfs and depauperate plants. He comes to the conclusion that the latter have smaller cells than normal, but finds three classes of inherited dwarfing; dwarfs of Pisum, Solanum, Zea and Clarkia have smaller cells than normal, those of Nigella larger cells than normal and those of Mirabilis and Lathyris cells of normal size. Unfortunately he does not record the size and number of chromosomes in the material investigated by him.

It is evident, accordingly, that not only may different types of size variations occur in different categories of tissues, but also in different

types of organisms and under different experimental or enviromental conditions. In certain tissues, in given species or groups of plants or animals, differences in growth or environment produce but slight fluctuations from the norm or inherited cell size. This is not true, however, for all types of cells under all conditions.

That the extensive investigations of the comparative anatomist may be of considerable assistance, as reconnaissance surveys, in the selection of suitable material for more intensive, experimental investigations, and to serve as checks upon too extensive generalization from limited induction, is indicated by the literature dealing with body size and cell size. For example, many difficulties might have been avoided if the work of Levi (1906), upon the size of the various tissue-cells in different groups of animals, particularly mammals, had preceded some of the earlier, more intensive investigations. Therefore, in undertaking a series of investigations upon the size variations of tracheary cells, it seems to be desirable to begin with a reconnaissance survey of cell size in the secondary xylem of vascular cryptogams, gymnosperms and angiosperms.

In selecting this tissue for investigation the writers are influenced by the following considerations: (1) Since the secondary xylem reaches its optimum development in trees, lianas and large shrubs, plants with a long reproductive cycle, it is a more favorable subject for the extensive investigations of the comparative anatomist than the more intensive cultural investigations of the geneticist. (2) From analogy with animal tissues, it seems probable that the dimensions of the highly differentiated tracheary cells of the secondary xylem may fluctuate considerably in response to physiological and environmental influences. (3) Inasmuch as this tissue is one of the most extensively used botanical raw products, an investigation of this character may throw some light upon a number of economic problems, particularly those in the field of the paper-pulp industry.

Material and Methods.

Most of the material, used in the preparation of the following tables, was secured from the extensive collections of the Bussey Institution and Arnold Arboretum. Since the samples of wood and herbarium specimens were collected at different times, and in different parts of the world, by a number of taxonomists and dendrologists, it seems to be advisable to tabulate them as far as possible under their original

names and authorities. Of course, these specimens are available for future study and comparison.

In dealing with a considerable number of specimens from various parts of the world, it is extremely difficult to be certain that every specimen has been assigned to the right species, and in some cases to the proper genus. Such errors may be extremely serious in certain types of investigations, but, as will be evident later, can have no appreciable effect upon the general conclusions reached in this paper. The plants are grouped into orders, families and subfamilies, according to the Engler and Gilg (1912) system of classification.

For the purposes of this investigation, simple and septate libriform fibers, as well as fiber-tracheids, tracheids and vessel-segments, are classified as tracheary elements. Fiber-tracheids and libriform fibers grade into one another and appear to be interchangeable in many plants. That is to say, in certain specimens or growth layers there are clearly differentiated bordering areas about the pits, whereas in others thay have almost if not entirely disappeared. Furthermore, it frequently is difficult to determine whether vestigial borders are present or not.

Lengths of tracheary elements were obtained from macerations; widths of vessel-segments, and notes in regard to the general structure of the xylem, from microtome sections ten micra in thickness. All measurements, from 10–100 depending upon the accuracy desired, were made with a standardized micrometer eyepiece. Averages of 50–100 measurements were used as basic points in plotting the graphs. The means given in Tables I and II are usually averages of 10 measurements. The probable errors of these means fluctuate between two and six percent.

Size Variation of secondary tracheary Elements in Stems of Gymnosperms and Dicotyledons.

In Tables I and II are recorded the lengths of the tracheary elements of a considerable number of gymnosperms and woody dicotyledons. Since the specimens, from which the measurements were made, were secured from different parts of stems, from plants of different ages, sizes, growth habits and systematic affinities, and from different types of environments in various phytogeographic regions of the earth, these data should give a fairly reliable indication of the general size variations that occur in the tracheary elements of the secondary xylem of the stems of conifers and arborescent and fruticose dicotyledons.

TABLE I.

GYMNOSPERMAE.

Secondary xylem: Length of Tracheids in Millimeters.

Designation			Older Wood			First Annual Ring.		
Plant	No.	Age*	Max.	Mean	Min.	Max.	Mean	Min.
I. CORDAITALES.								
1. Cordaitaceae.								
Callixylon Oweni Elk. & Wiel.				4.9+				
Mesoxylon poroxyloides Scott and Malsen				5.2+				
II. BENNETTITALES.								
2. Bennettitaceae.								
Cycadioidea Dartoni Wiel.				5.4+				
C. dacotensis Ward.				5.1+				
III. CYCADALES.								
3. Cycadaceae.								
Dioon spinulosum Dyer.	1528	O	*9.5*	6.8	*4.1*	*7.3*	5.5	*4.1*
Microcycas calocoma A. DC.						*6.3*	4.6	*3.9*
IV. GINKGOALES.								
4. Ginkgoaceae.								
Ginkgo biloba Linn.	707	O	*4.8*	3.5	*2.8*	*1.6*	0.9	*0.6*
V. CONIFERAE.								
5. Taxaceae.								
Podocarpoideae-Pherosphaereae.								
Pherosphaera Hookeriana Archer.						*0.9*	0.7	*0.6*

* Y = less than 20 rings from pith. M = 20–60 rings from pith. O = more than 60 rings from pith.

TABLE I — *Continued.*

Designation		Older Wood				First Annual Ring		
Plant	No.	Age*	Max.	Mean	Min.	Max.	Mean	Min.
Podocarpoideae-Podocarpeae.								
Dacrydium Bidwillii Hook. f.						*0.7*	0.5	*0.3*
Franklinii Hook. f.	726	O	*2.4*	1.9	*1.5*			
Microcachrys tetragona Hook. f.						*0.9*	0.7	*0.6*
Podocarpus bracteata Hort. ex Carr.						*1.3*	1.0	*0.7*
chinensis Sweet.	711	O	*3.7*	2.5	*1.2*			
elata R. Br.	712	O	*4.8*	3.3	*1.7*			
latifolia Wall.	758	O	*6.5*	5.1	*2.6*			
macrophylla D. Don.	C50	M	*3.2*	2.6	*2.3*			
Nageia R. Br.	703	M	*5.0*	3.7	*1.8*			
neriifolia D. Don.	719	M	*5.0*	3.9	*2.6*			
Saxegothaea conspicua Lindl.						*1.2*	1.0	*0.7*
Phyllocladoideae.								
Phyllocladus glauca T. Kirk.						*1.7*	1.2	*0.8*
Taxoideae-Cephalotaxeae.								
Cephalotaxus drupacea Sieb. & Zucc.						*1.1*	0.6	*0.5*
species.	1412	M	*2.7*	2.2	*1.5*			
Taxoideae-Taxeae.								
Taxus baccata Linn.	742	M	*3.1*	2.5	*2.2*			
brevifolia Nutt.	J92	M	*2.1*	1.7	*0.7*			
cuspidata Sieb. & Zucc.	756	M	*2.5*	2.0	*1.5*	*0.8*	0.6	*0.4*
floridana Nutt.	J91	M	2.4	1.9	1.5			
Torreya californica Torr.	J89	O	*3.1*	2.4	*1.4*			

nucifera Sieb. & Zucc.	776	O	*4.3*	3.2	*2.2*	*1.0*	0.7	*0.5*
taxifolia Arn.	761	M	*3.9*	3.2	*2.5*			
6. Pinaceae.								
Araucarieae.								
Agathis australis Steud.	727	O	*7.3*	5.4	*3.3*	*2.1*	1.5	*0.8*
robusta F. M. Bailey.	B10	O	*8.2*	7.1	*4.1*			
Araucaria Bidwillii Hook.	B11	M	*8.8*	6.4	*3.5*			
brasiliensis Loud.	B12	O	*9.4*	6.6	*2.3*			
Cunninghamii Sweet.	723	O	*10.9*	6.2	*2.5*	*1.7*	1.1	*0.7*
imbricata Pav.	B13	M	*4.7*	3.5	*2.2*			
Abieteae.								
Abies bracteata Hook. & Arn.	J528	M	*3.3*	2.7	*1.3*			
concolor Lindl. & Gord.	J56	M	*4.0*	2.5	*0.7*	*1.2*	0.9	*0.5*
firma Sieb. & Zucc.	779	M	*5.5*	4.5	*2.0*			
Fraseri Lindl.	J59	M	*3.9*	3.1	*2.1*			
grandis Lindl.	J723	Y	*4.2*	3.0	*1.8*			
lasiocarpa Hook.	J724	M	*2.7*	2.4	*1.3*			
Lowiana A. Murr.	J725	M	*3.9*	3.1	*1.9*			
magnifica A. Murr.	J62	M	*3.4*	2.5	*1.9*			
nobilis Lindl.	H726	O	*5.4*	4.4	*3.5*			
Nordmanniana Spach.						*1.0*	0.8	*0.6*
sibirica Ledeb.	J529	M	*3.5*	2.7	*1.7*			
venusta C. Koch.	J571	M	*4.0*	3.3	*1.3*			
Webbiana Lindl.	778	M	*4.1*	3.5	*2.8*			
Cedrus Deodara Loud.	789	O	*3.6*	2.9	*2.2*	*1.1*	0.8	*0.5*
Libani Barrel.	BM	O	*4.0*	3.0	*2.0*	*1.4*	0.8	*0.5*
Keteleeria Davidiana Beissn.	769	O	*5.6*	4.7	*2.2*	*1.8*	1.4	*1.1*
Larix dahurica Turcz.	J39	Y	*2.8*	2.4	*2.0*			
decidua Mill.	714	M	*4.9*	4.0	*3.3*	*1.2*	0.8	*0.5*
leptolepis Hort. ex Endl.	760	O	*5.3*	4.3	*3.3*	*1.1*	0.8	*0.4*
occidentalis Nutt.	J40	O	*5.6*	4.4	*1.9*			

TABLE I—*Continued.*

Designation		Older Wood				First Annual Ring.		
Plant	No.	Age*	Max.	Mean	Min.	Max.	Mean	Min.
Picea ajanensis Fisch.	J42	M	*4.6*	3.8	*2.5*			
alba Link.	H718	M	*4.4*	3.6	*2.7*			
Alcockiana Carr.	709	O	*5.3*	4.5	*3.1*			
canadensis Britton.	J43	M	*4.1*	3.4	*2.9*	*1.5*	1.0	*0.6*
Engelmanni Engelm.	J44	O	*4.1*	3.1	*1.5*			
excelsa Link.	J45	M	*2.4*	1.9	*1.5*	*1.1*	0.8	*0.5*
Mariana Britton.	J47	O	*3.9*	3.4	*2.7*	*0.9*	0.6	*0.4*
Morinda Link.	768	O	*5.2*	4.4	*3.3*			
obovata Ledeb.	J46	M	*4.1*	3.1	*2.0*			
polita Carr.	C46	M	*2.6*	1.9	*1.7*			
pungens Engelm.	J533	M	*3.4*	2.8	*1.8*			
rubens Sarg.	J48	O	*3.2*	2.6	*1.6*			
sitchensis Trautv. & Mey.	J50	M	*6.8*	5.6	*4.5*			
Pinus albicaulis Engelm.	H537	M	*4.3*	3.1	*2.0*			
aristata Engelm.	J1	M	*2.4*	1.8	*1.0*			
arizonica Engelm.	J3	Y	*2.2*	1.9	*1.7*			
attenuata Lemmon.	H565	O	*3.5*	3.0	*1.9*			
Balfouriana S. Wats.	J5	O	*2.8*	2.4	*2.2*			
Bungeana Zucc.	1124	Y	*3.2*	2.4	*1.6*			
cembra Linn.	705	O	*2.6*	2.0	*1.2*			
cembroides Zucc.	J6	M	*3.2*	2.5	*1.5*			
Chihuahuana Engelm.	J7	O	*5.5*	4.9	*2.5*			
clausa Vasey.	J8	Y	*3.7*	3.0	*2.4*			

contorta Dougl.	H579	M	*3.7*	3.1	*2.6*	*1.3*	1.0	*0.7*
contorta var. *Murrayana* Engelm.	J22	M	*3.9*	2.9	*2.2*			
Coulteri D. Don.	J10	M	*3.1*	2.5	*1.4*			
cubensis Griseb.	J11	O	*6.0*	4.9	*3.5*			
densiflora Sieb. & Zucc.	C12	O	*5.6*	4.9	*3.9*			
divaricata Hort. ex Gord.	H714	Y	*2.6*	2.0	*1.3*			
edulis Engelm.	J14	O	*3.6*	2.9	*2.4*			
excelsa Wall.	641	M	*5.2*	4.3	*3.0*			
flexilis James.	J16	O	*3.8*	3.2	*2.9*	*1.1*	0.8	*0.5*
Gerardiana Wall.	750	O	*4.2*	3.8	*2.6*			
glabra Walt.	J17	M	*6.5*	5.3	*4.6*			
insularis Endl.	739	M	*5.2*	4.6	*2.9*			
Jeffreyi A. Murr.	J18	O	*5.9*	4.6	*3.6*			
Lambertiana Dougl.	J19	O	*5.5*	4.4	*2.7*			
Laricio Poir.	728	M	*4.5*	3.7	*2.6*			
longifolia Roxb.	746	M	*6.2*	4.5	*3.7*			
macrophylla Engelm.	J20		*5.0*	4.4	*4.0*			
Massoniana D. Don.	749	O	*5.7*	4.7	*3.5*			
Merkusii Jungh. & De Vriese.	741	M	*6.9*	5.2	*3.5*			
monophylla Torr. & Frém.	H566	O	*4.9*	3.1	*2.4*			
monticola Dougl.	H539	O	*6.0*	5.2	*3.9*			
muricata D. Don.	J21	M	*4.0*	3.2	*1.7*			
palustris Mill.	H526	M	*4.6*	3.6	*1.5*			
parviflora Sieb. & Zucc.	722	O	*5.9*	4.4	*3.0*			
ponderosa Dougl.	J26	O	*3.8*	3.3	*2.2*	*1.0*	0.8	*0.5*
Pumilio Haenke.	J24	Y	*2.4*	1.9	*1.3*			
pungens Lamb.	H575	M	*5.0*	4.0	*1.8*			
quadrifolia Parry.	H540	M	*4.0*	2.5	*1.4*			
reflexa Engelm.	J28	M	*4.0*	3.1	*1.3*			
resinosa Ait.	J29	M	*3.2*	2.7	*1.8*	*1.3*	1.0	*0.7*

TABLE I—*Continued.*

Designation		Older Wood				First Annual Ring.		
Plant	No.	Age*	Max.	Mean	Min.	Max.	Mean	Min.
Pinus rigida Mill.	J30	O	*5.3*	4.0	*3.2*			
Sabiniana Dougl.	J32	Y	*3.5*	2.9	*2.3*			
serotina Michx.	J33	M	*6.1*	4.5	*2.8*			
Strobus Linn.	J34	M	*5.0*	3.9	*2.3*	*1.1*	0.8	*0.6*
sylvestris Linn.	715	M	*3.9*	3.2	*2.2*	*1.0*	0.7	*0.5*
Taeda Linn.	J70	M	*7.3*	5.4	*3.6*	*1.7*	1.4	*0.9*
Thunbergii Parl.	708	M	*4.8*	3.6	*2.9*			
Torreyana Parry.	J35	M	*5.3*	3.9	*2.4*			
tuberculata Gord.	J37	M	*3.4*	3.0	*2.8*			
Pseudolarix Kaempferi Gord.						*1.2*	1.0	*0.5*
Pseudotsuga macrocarpa Lemmon.	762	M	*3.4*	3.1	*2.1*			
taxifolia Britton.	J54	M	*4.2*	2.6	*1.8*	*1.2*	0.8	*0.5*
Tsuga canadensis Carr.	SB	M	*4.3*	3.2	*1.9*			
caroliniana Engelm.	J51	M	*3.5*	3.1	*2.5*	*1.2*	0.9	*0.5*
formosana Hayata.	710	O	*5.4*	3.5	*1.4*			
Mertensiana Carr.	J53	O	*4.6*	3.7	*2.5*			
Sieboldii Carr.	699	O	*4.8*	4.0	*3.0*			
Taxodieae								
Athrotaxis selaginoides D. Don.						*1.4*	1.1	*0.9*
Cryptomeria japonica D. Don.	C41	O	*3.7*	2.7	*1.9*	*0.9*	0.7	*0.4*
Cunninghamia sinensis R. Br.						*1.5*	1.1	*0.6*
Glyptrostrobus heterophyllus Endl.						*1.4*	1.0	*0.6*
Sciadopitys verticillata Sieb. & Zucc.	759	O	*3.8*	3.2	*2.5*	*1.2*	0.9	*0.6*

Sequoia gigantea Lindl. & Gord.	J66	O	*5.4*	4.6	*3.0*			
Idem.	B14	O	*4.1*	2.9	*2.1*			
Idem.	J67	O	*7.0*	5.0	*3.7*			
sempervirens Endl.	B15	M	*9.2*	6.4	*2.6*	*1.3*	1.0	*0.7*
Idem.	B16	O	*8.4*	6.5	*4.1*			
Taiwania cryptomerioides Hayata.	721	M	*6.7*	5.7	*5.1*	*1.4*	1.1	*0.7*
Taxodium distichum Rich.	J65	M	*5.6*	4.1	*1.5*	*1.1*	0.8	*0.6*
Idem.	H727	O	7.8	6.5	3.5			
Cupresseae-Actinostrobinae.								
Actinostrobus pyramidalis Miq.						*1.2*	0.9	*0.7*
Callitris calcarata R. Br.	757	O	*3.5*	2.7	*1.9*	*1.0*	0.8	*0.5*
Cupresseae-Thujopsidinae.								
Libocedrus decurrens Torr.	J69	M	*3.8*	3.2	*2.7*	*0.8*	0.7	*0.6*
macrolepis Benth. & Hook.	763	O	*4.4*	3.5	*2.3*			
Thuja japonica Maxim.	698	O	*4.1*	3.4	*2.8*			
occidentalis Linn.	J71	M	*2.9*	2.2	*1.3*	*0.9*	0.7	*0.6*
plicata Donn.	J530	O	*3.2*	2.6	*1.8*			
Idem.	H728	O	*4.0*	3.2	*2.0*			
Idem.	B17	O	*5.4*	4.7	*4.0*			
Thujopsis dolabrata Hort.						*1.3*	0.9	*0.7*
Cupresseae-Cupressinae.								
Chamaecyparis formosensis Matsum.	752	O	*4.9*	3.7	*2.7*			
Lawsoniana Parl.	J76	O	*4.1*	3.4	*2.7*			
nootkatensis Lamb.	J77	O	*3.2*	2.8	*2.2*			
obtusa Sieb. & Zucc.	745	O	*5.4*	3.7	*2.1*			
thyoides Sarg.	J78	M	*4.7*	3.8	*2.9*	*0.9*	0.7	*0.5*
Cupressus arizonica Greene.	J561	M	*2.1*	1.5	*1.1*			
Goveniana Gord.	H559	M	*3.3*	2.6	*2.0*			
guadalupensis S. Wats.	702	O	*2.4*	2.1	*1.7*			
Macnabiana A. Murr.	J75	O	*2.6*	2.0	*1.5*	*1.1*	0.8	*0.6*
macrocarpa Hartw.	J74	M	*3.8*	3.2	*2.8*			

TABLE I — *Concluded.*

Designation		Older Wood				First Annual Ring		
Plant	No.	Age*	Max.	Mean	Min.	Max.	Mean	Min.
Juniperus barbadensis Linn.	J79	O	*3.2*	2.7	*1.7*			
bermudiana Linn.	J81	M	*3.7*	2.3	*1.4*			
californica Carr.	J83	O	*2.4*	2.0	*1.6*			
chinensis Linn.	C11	O	*2.0*	1.7	*1.2*			
macropoda Boiss.	720	O	*3.0*	2.6	*1.8*			
occidentalis Hook.	J84	O	*2.2*	1.8	*1.1*			
pachyphlaea Torr.	J86	O	*2.8*	2.2	*1.6*			
scorpulorum Sarg.	J87	M	*2.7*	2.2	*1.5*			
virginiana Linn.	H732	M	*2.8*	2.0	*1.3*	*0.9*	0.6	*0.4*

TABLE II.

ANGIOSPERMAE-DICOTYLEDONEAE.

Secondary Xylem: Length of Tracheary Elements in Millimeters.

Designation		Older Wood								First Annual Ring	
		Type†	Age*	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
A. Archichlamydeae											
I. Verticillatae.											
1. Casuarinaceae.											
Casuarina torulosa Ait.	1481	II	O	*0.7*	0.6	*0.4*	*1.4*	1.0	*0.7*		
II. Piperales.											
2. Piperaceae.											
Cubeba officinalis Rafin.	1077	IV	Y	*0.4*	0.3	*0.2*	*0.6*	0.5	*0.4*		
Macropiper excelsum Miq.	665	IV	Y	*0.4*	0.2	*0.1*	*0.9*	0.7	*0.6*		
3. Chloranthaceae.											
Chloranthus officinalis Blume.	1092	I	Y	*1.1*	0.8	*0.4*	*1.2*	0.9	*0.6*		
III. Salicales.											
4. Salicaceae.											
Populus grandidentata Michx.	J135	III	M	*0.9*	0.7	*0.5*	*1.5*	1.3	*1.0*	0.4	0.5
Salix alba Linn.	584	IV	M	*0.6*	0.5	*0.4*	*1.2*	0.9	*0.7*		

* Y = less than 15 years from pith. O = more than 30 years from pith. M = 15–30 years from pith.
† See page 190.

TABLE II—*Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
IV. Myricales.											
5. Myricaceae.											
Myrica californica Cham. & Schlecht.	J106	I	M	*0.9*	0.7	*0.5*	*1.3*	1.0	*0.8*		
V. Leitneriales.											
6. Leitneriaceae.											
Leitneria floridana Chapm.	361	IV	M	*0.8*	0.6	*0.5*	*1.1*	0.7	*0.5*		
VI. Juglandales.											
7. Juglandaceae.											
Carya ovata (Mill) K. Koch.	PB	IV	O	*0.6*	0.5	*0.4*	*1.5*	1.1	*0.8*	0.3	0.7
Engelhardtia spicata Blume.	279	IV	O	*0.9*	0.7	*0.5*	*1.8*	1.5	*1.2*		
Juglans cinerea Linn.	J513	IV	O	*0.6*	0.4	*0.3*	*1.6*	1.1	*0.8*		
VII. Fagales.											
8. Betulaceae.											
Alnus rubra Bongard.	J149	I	O	*0.9*	0.8	*0.6*	*1.4*	1.1	*1.0*	0.6	0.7
Betula lutea Michx.	J139	I	O	*1.5*	1.2	*0.9*	*2.1*	1.7	*1.1*		
Corylus rostrata Ait.	J507	I	Y	*0.7*	0.5	*0.4*	*1.1*	0.9	*0.7*	0.5	0.7
9. Fagaceae.											
Castanea vesca Gaertn.	240	IV	O	*0.8*	0.7	*0.5*	*1.2*	1.0	*0.7*	0.3	0.5
Fagus ferruginea Ait.	J153	IV	O	*0.7*	0.6	*0.4*	*1.4*	1.2	*0.9*	0.3	0.6
Quercus Kelloggii Newberry.	J187	IV	O	*0.6*	0.5	*0.4*	*1.5*	1.0	*0.7*	0.5	0.7

VIII. Urticales.											
10. Ulmaceae.											
Holoptelea integrifolia Planch.	618	IV	O	*0.4*	0.3	*0.2*	*1.2*	1.0	*0.8*		
Planera aquatica J. F. Gmel.	J203	IV	M	*0.3*	0.2	*0.2*	*1.5*	1.2	*.9*		
Ulmus americana Linn.	610	IV	O	*0.3*	0.2	*0.1*	*1.3*	1.1	*0.8*	0.2	0.4
Zelkova acuminata Planch.	619	IV	O	*0.3*	0.2	*0.2*	*2.3*	1.9	*1.6*		
11. Moraceae.											
Artocarpus incisa Linn. f.	925	IV	Y	*0.7*	0.6	*0.5*	*2.1*	1.9	*1.5*		
Castilloa fallax O. F. Cook.	1594	IV	M	*0.5*	0.4	*0.3*	*1.5*	1.1	*0.8*		
Morus alba Linn.	H643	IV	M	*0.3*	0.2	*0.2*	*1.2*	0.8	*0.7*	0.2	0.4
12. Urticaceae.											
Boehmeria rugulosa Wedd.	1002	IV	O	*0.5*	0.3	*0.2*	*2.0*	1.4	*0.8*		
Neraudia melastomaefolia Mus. Par. ex Blume.	943	III	M	*1.1*	1.0	*0.8*	*1.7*	1.5	*1.1*		
Pipturus albidus A. Gray.	940	IV	M	*0.4*	0.2	*0.1*	*1.1*	0.9	*0.6*		
IX. Proteales.											
13. Proteaceae.											
Banksia verticillata R. Br.	496	IV	M	*0.5*	0.4	*0.3*	*1.8*	1.5	*1.0*		
Grevillea robusta A. Cunn.	498	IV	M	*0.5*	0.4	*0.3*	*2.1*	1.6	*1.0*		
Hakea leucoptera R. Br.	499	IV	M	*0.4*	0.3	*0.2*	*1.8*	1.5	*1.1*		
X. Santalales.											
14. Santalaceae.											
Santalum ellipticum Gaudich.	914	IV	M	*0.4*	0.3	*0.2*	*1.1*	1.0	*0.7*		
Cygnorum Miq.	569	IV	M	*0.4*	0.2	*0.1*	*0.8*	0.5	*0.3*		
15. Olacaceae.											
Olax imbricata Roxb.	1091	IV	Y	*0.5*	0.3	*0.2*	*1.3*	1.0	*0.8*		
15a. Loranthaceae											
Tupeia antarctica Cham. & Schlecht.	1173	IV	Y	*0.1*	0.1	*0.1*	*0.5*	0.4	*0.2*		
XI. Aristolochiales.											
16. Aristolochiaceae.											
Aristolochia tricaudata Lem.	1039	IV	Y	*0.4*	0.3	*0.2*	*1.1*	1.0	*0.8*		
tomentosa Sims.	666	IV	Y	*0.3*	0.2	*0.2*	*0.7*	0.6	*0.4*		

TABLE II — *Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
XII. Polygonales.											
17. Polygonaceae.											
Coccoloba uvifera Linn.	J215	IV	M	*0.4*	0.4	*0.3*	*0.9*	0.7	*0.4*	0.3	0.4
XIII. Centrospermae.											
18. Chenopodiaceae.											
Atriplex species.	828	IV	M	*0.1*	0.1	*0.1*	*0.4*	0.3	*0.2*		
Kochia pyramidata Benth.	1340	IV	M	*0.1*	0.1	*0.1*	*0.4*	0.3	*0.2*		
Suaeda fruticosa Hook & Arn.	1075	IV	M	*0.1*	0.1	*0.1*	*0.4*	0.3	*0.2*		
19. Amarantaceae.											
Charpentiera ovata Gaudich.	1000	IV	M	*0.3*	0.3	*0.2*	*1.1*	0.8	*0.5*	0.2	0.3
Nototrichum sandwicense Hillebr.	995	IV	O	*0.2*	0.1	*0.1*	*0.6*	0.5	*0.4*		
20. Nyctaginaceae.											
Pisonia obtusata Jacq.	J95	IV	O	*0.1*	0.1	*0.1*	*0.8*	0.6	*0.4*		
21. Phytolaccaceae.											
Seguieria Langsdorffii Moq.	1568	IV	O	*0.4*	0.3	*0.2*	*1.2*	0.9	*0.7*		
XIV. Ranales.											
22. Trochodendraceae.											
Trochodendron aralioides Sieb. & Zucc.	1765		O				*6.0*	4.5	*2.8*		2.2
23. Cercidiphyllaceae.											

Cercidiphyllum japonicum Sieb. & Zucc.	607	I	O	*2.0*	1.6	*1.4*	*2.2*	1.9	*1.4*	0.7	0.7+
24. Ranunculaceae.											
Clematis indivisa Willd.	1160	IV	M	*0.5*	0.4	*0.2*	*0.7*	0.5	*0.4*		
Paeonia Moutan Sims	771	I	M	*0.4*	0.3	*0.2*	*0.6*	0.4	*0.3*		
25. Berberidaceae.											
Berberis Fremontii Torr.	J497	IV	M	*0.3*	0.2	*0.1*	*0.5*	0.4	*0.3*		
26. Menispermaceae.											
Saccopetalum tomentosum Hook. f. & Thoms.	489	IV	M	*0.5*	0.4	*0.2*	*1.3*	1.1	*0.8*		
27. Magnoliaceae.											
Drimys Winteri Forst.	B18		O				*5.1*	4.3	*3.5*		1.6
Illicium anisatum Gaertn.	1668	I								0.8	0.9
Kadsura scandens Blume.	1514	II	Y		1.1			1.6			
Liriodendron tulipifera Linn.	1658	I	O	*1.5*	1.1	*0.7*	*2.8*	2.3	*1.7*	0.5	0.6
Magnolia acuminata Linn.	1653	II	O	*1.1*	0.8	*0.6*	*2.1*	1.6	*0.9*	0.6	0.8
Michelia Champaca Linn.	477	I	O	*1.2*	0.8	*0.7*	*1.8*	1.4	*0.8*		
Tetracentron sinense Oliver.	1500										1.8
28. Anonaceae.											
Anona laurifolia Dunal.	4	IV	M	*0.5*	0.4	*0.3*	*1.5*	1.3	*0.7*		
Cyathocalyx globosus Merrill.	8	IV	O	*0.8*	0.6	*0.3*	*2.0*	1.5	*1.4*		
Polyalthia flava Merrill.	6	IV	O	*0.4*	0.3	*0.2*	*1.6*	1.2	*0.8*		
29. Myristicaceae.											
Myristica philippensis Lam.	487	I	O	*1.6*	1.2	*0.7*	*1.7*	1.4	*1.1*		
Virola species.	1622	II	M		1.0			1.5			
30. Monimiaceae.											
Doryphora Sassafras Endl.	481	I	O		1.0			1.6		0.5	0.8
Hedycarya arborea Forst.	480	I	O		1.5			1.8			
Laurelia Novae-Zelandiae A. Cunn.	479	I	O		1.4			1.6		0.9	1.0
31. Lauraceae.											
Beilschmiedia Cairocan Vidal.	343	IV	O	*0.9*	0.8	*0.7*	*2.0*	1.6	*1.3*		

TABLE II—*Continued.*

Designation				Older Wood						First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
Cryptocarya Mannii Hillebr.	966	IV	M	*0.6*	0.5	*0.4*	*1.3*	1.1	*0.9*		
Sassafras officinale Nees & Eberm.	NN	IV	O	*0.5*	0.4	*0.3*	*1.1*	0.8	*0.7*	0.3	0.4
32. Hernandiaceae.											
Gyrocarpus americanus Jacq.	272	IV	O	*0.5*	0.3	*0.2*	*1.2*	1.0	*0.6*		
Jacquini Gaertn.	273	IV	O	*0.5*	0.4	*0.2*	*1.0*	0.9	*0.7*		
XV. Rhoeadales.											
33. Papaveraceae.											
Dendromecon rigidum Benth.	680	IV	Y	*0.6*	0.4	*0.2*	*0.7*	0.6	*0.4*		
34. Capparidaceae.											
Capparis jamaicensis Jacq.	J104	IV	O	*0.3*	0.2	*0.1*	*0.6*	0.2	*0.3*	0.2	0.2+
Crataeva Tapia Linn.	1561	IV	M	*0.4*	0.3	*0.2*	*1.0*	0.8	*0.7*		
XVI. Rosales.											
35. Saxifragaceae.											
Brexia serrata Presl.	1066	III	M	*0.8*	0.6	*0.4*	*1.2*	1.0	*0.7*		
Ceratopetalum apetalum D. Don.	566	II	O	*1.1*	0.9	*0.6*	*1.4*	1.3	*0.9*		
Hydrangea quercifolia Bartram.	J234	I	Y	*1.6*	1.1	*0.7*	*2.0*	1.6	*1.0*		
36. Pittosporaceae.											
Pittosporum bicolor Hook.	1419	III	M	*0.6*	0.5	*0.3*	*0.9*	0.8	*0.6*		
Buchanani Hook. f.	507	III	M	*0.8*	0.7	*0.4*	*1.0*	0.8	*0.6*		
cornifolium A. Cunn.	1151	III	M	*0.6*	0.5	*0.4*	*0.8*	0.7	*0.6*		

37. Cunoniaceae.											
Weinmannia racemosa Linn.	567	I	O	*1.2*	0.8	*0.6*	*1.2*	1.0	*0.8*		
rubifolia Benth.	568	IV	O	*0.7*	0.6	*0.5*	*1.5*	1.3	*1.1*		
38. Hamamelidaceae.											
Altingia excelsa Noronha.	875	I	O	*2.3*	1.9	*1.2*	*3.1*	2.8	*2.0*	0.7	1.0
Bucklandia populnea R. Br.	880	I	O	*2.4*	1.6	*1.2*	*3.2*	2.7	*1.6*	0.8	1.0
Distylium species	773	I	O	*1.2*	0.9	*0.7*	*1.7*	1.4	*1.0*		
Hamamelis virginiana Linn.	J235	I	O	*1.1*	0.8	*0.5*	*1.6*	1.1	*0.8*	0.5	0.6
39. Platanaceae.											
Platanus occidentalis Linn.	N825	II	O	*0.8*	0.5	*0.3*	*1.9*	1.6	*1.0*	0.3	0.7
40. Rosaceae.											
Crataegus cordata Ait.	J251	IV	M	*0.6*	0.5	*0.2*	*1.3*	1.0	*0.8*		
Prunus serotina Ehrh.	J269	IV	O	*0.6*	0.5	*0.4*	*1.8*	1.4	*1.1*	0.3	0.4
Pygeum Preslii Merrill.	518	IV	O	*0.7*	0.5	*0.4*	*1.8*	1.4	*0.9*		
41. Leguminosae.											
Bauhinia purpurea Linn.	1363	IV	O	*0.3*	0.3	*0.2*	*1.6*	1.2	*1.1*		
Cercis canadensis Linn.	J286	IV	O	*0.3*	0.2	*0.2*	*1.4*	1.0	*0.7*	0.2	0.4
Wallaceodendron celebicum Koord.	341	IV	O	*0.5*	0.4	*0.3*	*1.4*	1.1	*0.8*		
XVII. Geraniales.											
42. Oxalidaceae.											
Averrhoa Species.	1105	IV	M	*0.4*	0.3	*0.2*	*0.6*	0.5	*0.4*		
43. Erythroxylaceae.											
Erythroxylum monogynum Roxb.	175	IV	M	*0.7*	0.4	*0.2*	*1.4*	1.1	*0.9*		
44. Zygophyllaceae.											
Larrea mexicana Moric.	J108	IV	M	*0.3*	0.2	*0.2*	*0.8*	0.6	*0.5*	0.2	0.4
Guaiacum officinale Linn.	1032	IV	O	*0.2*	0.1	*0.1*	*0.7*	0.5	*0.3*		
45. Rutaceae.											
Platydesma campanulata H. Mann.	923	III	M	*0.7*	0.5	*0.3*	*1.2*	1.0	*0.7*		
Ptelea trifoliata Linn.	J312	IV	M	*0.4*	0.2	*0.1*	*1.0*	0.8	*0.5*		
Xanthoxylum Species.	1613	IV	M	*0.7*	0.6	*0.5*	*1.6*	1.2	*0.7*		

TABLE II—*Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
46. Simarubaceae.											
Ailanthus philippinensis Merrill.	583	IV	O	*0.6*	0.5	*0.3*	*1.6*	1.3	*1.0*		
Simaruba glauca DC.	J315	IV	O	*0.7*	0.6	*0.5*	*1.1*	1.0	*0.7*	0.3	0.6
47. Burseraceae.											
Bursera Simaruba Sarg.	J101	IV	M	*0.8*	0.5	*0.4*	*1.3*	1.0	*0.6*	0.3	0.4
Canarium ovatum Engl.	50	IV	O	*0.8*	0.6	*0.4*	*1.6*	1.3	*1.0*		
48. Meliaceae.											
Aglaia Clarkii Merrill.	442	IV	O	*0.8*	0.6	*0.4*	*1.6*	1.3	*0.9*		
Swietenia Mahogoni Jacq.	J319	IV	M	*0.5*	0.4	*0.3*	*1.3*	1.0	*0.7*	0.3	0.4
Xylocarpus obovatus A. Juss.	457	IV	O	*0.4*	0.3	*0.2*	*1.1*	0.9	*0.8*		
49. Malpighiaceae.											
Byrsonima Cumingana A. Juss.	1650	III	M	*0.8*	0.7	*0.4*	*1.9*	1.6	*1.0*		
50. Polygalaceae.											
Xanthophyllum flavescens Roxb.	512	IV	O	*0.8*	0.5	*0.3*	*1.0*	0.8	*0.4*		
species.	511	IV	M	*0.8*	0.5	*0.3*	*1.3*	1.1	*0.8*		
51. Euphorbiaceae.											
Antidesma edule Merrill.	159	IV	M	*1.0*	0.8	*0.5*	*1.8*	1.4	*1.0*	0.5	0.8
Aporosa sympocosifolia Merrill.	158	IV	M	*1.1*	0.9	*0.6*	*2.9*	2.1	*1.3*		
Ricinus communis Linn.	H644	IV	M	*0.7*	0.5	*0.4*	*1.4*	1.1	*0.7*		
Sapium jamaicense Sw.	1627	IV	M	*0.9*	0.7	*0.4*	*1.5*	1.3	*0.8*		

XVIII. Sapindales.											
52. Coriariaceae.											
Coriaria ruscifolia Linn.	88	IV	M	*0.3*	0.2	*0.2*	*1.0*	0.8	*0.6*		
53. Anacardiaceae.											
Dracontomelon Cumingianum Baill.	16	IV	O	*0.9*	0.8	*0.6*	*1.6*	1.4	*1.1*		
Rhus typhina Linn.	J334	IV	M	*0.3*	0.2	*0.1*	*0.8*	0.6	*0.4*	0.2	0.3
Spondias mangifera Willd.	821	IV	O	*0.6*	0.5	*0.4*	*1.4*	1.0	*0.7*		
54. Cyrillaceae.											
Cliftonia monophylla Britton.	J339	I	O	*1.0*	0.8	*0.6*	*1.3*	1.0	*0.6*		
Cyrilla racemiflora Linn.	J338	I	O	*0.9*	0.8	*0.6*	*1.1*	1.0	*0.9*		
55. Aquifoliaceae.											
Byronia sandwicensis Endl.	959	I	O	*1.6*	1.3	*1.1*	*2.6*	2.0	*1.5*	0.7	1.0
Ilex opaca Ait.	N797	I	O	*1.0*	0.9	*0.8*	*1.8*	1.3	*0.9*	0.6	0.7
56. Celastraceae.											
Euonymus atropurpureus Jacq.	J348	IV	M	*0.8*	0.6	*0.4*	*0.9*	0.8	*0.7*		
Lophopetalum Wallichii Kurz.	182	IV	M	*1.4*	0.9	*0.4*	*1.9*	1.6	*0.9*		
Perrottetia sandwicensis A. Gray.	928	I	M	*1.1*	1.0	*0.8*	*1.5*	1.2	*0.7*	0.8	0.9
57. Salvadoraceae.											
Salvadora oleoides Decne.	556	IV	O	*0.2*	0.2	*0.1*	*0.8*	0.6	*0.4*		
58. Staphyleaceae.											
Turpinia nepalensis Wall.	564	I	O	*2.1*	1.4	*0.9*	*2.5*	1.9	*1.1*	0.9	1.0
59. Icacinaceae.											
Gonocaryum species.	276	III	O	*1.1*	0.8	*0.6*	*2.8*	2.4	*2.0*		
Pennantia corymbosa Forst.	277	III	O	*0.8*	0.7	*0.5*	*1.3*	1.0	*0.7*		
Stemonurus secundiflorus Blume.	1101	I	Y	*1.9*	1.6	*1.3*	*2.4*	2.0	*1.6*	0.8	1.2
Urandra luzoniensis Merrill.	278	I	O	*1.7*	1.4	*1.1*	*3.7*	3.3	*2.7*	0.9	1.1
Villaresia Moorei F. Muell.	494	I	O	*2.0*	1.6	*1.0*	*3.4*	2.9	*2.6*		
60. Aceraceae.											
Acer saccharinum Wangenh.	J358	IV	O	*0.5*	0.4	*0.3*	*0.8*	0.6	*0.5*	0. 2	0.4
61. Hippocastanaceae.											
Aesculus glabra Willd.	J366	IV	O	*0.5*	0.4	*0.3*	*1.1*	0.9	*0.7*	0.3	0.5

TABLE II —*Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
62. Sapindaceae.											
Dodonaea viscosa Jacq.	921	IV	M	*0.4*	0.3	*0.2*	*1.0*	0.9	*0.7*		
Pometia pinnata Forst.	562	IV	O	*0.5*	0.4	*0.2*	*1.2*	0.9	*0.7*		
Sapindus marginatus Willd.	J372	IV	O	*0.3*	0.2	*0.2*	*1.7*	1.2	*0.6*	0.2	0.4
63. Sabiaceae.											
Meliosma Arnottiana Walp.	551	I	O	*1.3*	1.2	*1.0*	*2.1*	1.5	*1.1*		
XIX. Rhamnales.											
64. Rhamnaceae.											
Rhamnus cathartica Linn.	J383	IV	O	*0.4*	0.3	*0.2*	*0.9*	0.7	*0.4*	0.3	0.4
Zizyphus zonulatus Blanco.	546	IV	O	*1.0*	0.7	*0.4*	*1.3*	1.1	*0.8*		
65. Vitaceae.											
Leea aculeata Blume.	1103	II	Y	*1.0*	0.8	*0.5*	*2.0*	1.4	*0.9*		
Vitis californica Benth.	J510	IV	M	*0.9*	0.7	*0.6*	*1.1*	0.9	*0.6*		
XX. Malvales.											
66. Elaeocarpaceae.											
Echinocarpus dasycarpus Benth.	149	III	M	*1.1*	1.0	*0.8*	*1.7*	1.4	*1.2*		
Elaeocarpus bifida Hook. & Arn.	918	III	O	*1.0*	0.9	*0.7*	*1.4*	1.2	*1.0*	0.4	0.5
Muntingia Calabura Linn.	156	IV	M	*0.4*	0.3	*0.2*	*1.8*	1.3	*1.0*		
Sloanea species.	1556	IV	M	*1.0*	0.8	*0.7*	*1.5*	1.2	*1.0*		

67. Tiliaceae.											
Grewia stylocarpa Warb.	601	III	M	*0.8*	0.7	*0.6*	*2.0*	1.6	*1.4*		
Tilia americana Linn.	N840	IV	O	*0.5*	0.4	*0.3*	*1.5*	1.1	*0.8*	0.3	0.7
68. Malvaceae.											
Bombycidendron Vidalianum Merrill. & Rolfe	474	IV	O	*0.4*	0.3	*0.2*	*2.0*	1.7	*0.8*		
Gossypium drynarioides Seem.	926	IV	M	*0.4*	0.3	*0.2*	*1.0*	0.7	*0.5*		
Thespesia populnea Soland.	471	IV	O	*0.4*	0.3	*0.2*	*1.6*	1.2	*0.9*		
69. Bombacaceae.											
Bombax malabaricum DC.	40	IV	O	*0.5*	0.4	*0.3*	*2.0*	1.6	*1.2*		
Cumingia philippinensis Vidal.	41	IV	O	*0.4*	0.4	*0.3*	*0.9*	0.8	*0.6*		
Ochroma Lagopus Sw.	1485	IV	O	*0.6*	0.4	*0.2*	*1.4*	1.0	*0.7*		
70. Sterculiaceae.											
Fremontia californica Torr.	J100	IV	O	*0.3*	0.2	*0.1*	*1.7*	1.6	*1.5*		
Heritiera littoralis Ait.	588	IV	M	*0.4*	0.3	*0.2*	*1.8*	1.4	*1.0*		
Kleinhovia Hospita Linn.	589	IV	O	*0.5*	0.4	*0.3*	*1.3*	1.0	*0.8*		
Sterculia crassiramea Merrill.	594	IV	O	*0.6*	0.5	*0.3*	*2.5*	1.9	*1.1*		
XXI. Parietales.											
71. Dilleniaceae.											
Curatella americana Linn.	1599	II	M	*1.0*	0.7	*0.5*	*2.4*	2.1	*1.4*		
Dillenia pentagyna Roxb.	102	I	M	*1.6*	1.2	*0.9*	*2.7*	2.1	*1.2*		
philippinensis Rolfe.	104	I	O	*2.3*	1.6	*1.0*	*3.4*	2.8	*2.2*	0.9	1.3
Saurauja Oldhami Hemsl.	105	I	M	*2.4*	2.0	*1.6*	*3.4*	2.9	*2.7*	1.3	1.6
Wormia excelsa Jack.	1059	I	Y	*2.3*	1.6	*0.7*	*3.0*	2.6	*2.0*	0.8	1.3
72. Ochnaceae.											
Cespedesia macrophylla Seem.	1640	IV	O	*0.7*	0.5	*0.4*	*1.4*	1.2	*1.0*		
73. Theaceae.											
Gordonia Lasianthus Linn.	J324	I	O	*1.7*	1.3	*1.0*	*1.8*	1.6	*1.2*	0.8	0.9
Schima Wallichii Choisy.	998	I	O	*1.6*	1.4	*1.2*	*2.9*	2.3	*1.6*	0.9	1.0
Ternstroemia japonica Thunb.	609	I	O	*1.5*	1.2	*0.9*	*2.4*	1.8	*1.4*	0.8	0.9
Thea japonica Baill.	1236	I	O	*0.9*	0.7	*0.6*	*2.0*	1.7	*1.0*	0.6	0.8

TABLE II—*Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
74. Guttiferae.											
Calophyllum Inophyllum Linn.	889	IV	M	*0.8*	0.6	*0.4*	*1.4*	1.2	*0.9*		
Cratoxylon floribundum F. Vill.	191	IV	M	*0.4*	0.4	*0.2*	*1.2*	1.1	*0.9*		
Kayea paniculata Merrill.	192	IV	O	*1.1*	0.8	*0.5*	*1.7*	1.3	*0.9*		
Symphoria globulifera Linn.	1572	IV	M	*0.8*	0.6	*0.4*	*1.9*	1.7	*1.4*		
75. Dipterocarpaceae.											
Dipterocarpus affinis Brandis.	112	IV	O	*0.9*	0.7	*0.5*	*2.1*	1.8	*1.4*		
Hopea acuminata Merrill.	114	IV	O	*0.5*	0.4	*0.3*	*1.9*	1.5	*1.0*	0.2	0.4
Shorea species.	123	IV	O	*0.6*	0.4	*0.3*	*1.5*	1.2	*0.9*		
76. Tamaricaceae.											
Tamarix articulata Vahl.	1072	IV	M	*0.2*	0.2	*0.1*	*1.0*	0.9	*0.6*		
77. Fouquieraceae.											
Fouquieria splendens Engelm.	856	IV	M	*0.4*	0.3	*0.2*	*1.4*	1.1	*0.7*		
78. Cistaceae.											
Cistus monspeliensis Linn.	1171	IV	M	*0.5*	0.3	*0.2*	*0.6*	0.4	*0.3*		
79. Winteranaceae.											
Canella Winterana Gaertn.	J99	I	O	*1.5*	1.2	*1.0*	*1.9*	1.5	*1.0*		
80. Violaceae.											
Alsodeia Roxburghii Hook. f. & Thoms.	1055	II	Y	*0.9*	0.8	*0.6*	*1.4*	1.0	*0.8*		

Hymenanthera Banksii F. Muell.	1422	III	Y	*0.5*	0.4	*0.3*	*0.7*	0.5	*0.4*		
Melicytus ramiflorus Forst.	636	II	Y	*1.1*	0.9	*0.6*	*1.6*	1.2	*0.9*		
81. Flacourtiaceae.											
Casearia glomerata Roxb.	181	III	O	*1.2*	1.0	*0.9*	*1.9*	1.6	*1.2*	0.8	1.1
Homalium luzoniense F. Villar.	178	III	M	*1.3*	1.1	*0.9*	*2.1*	1.6	*1.1*	0.5	0.6
Myroxylon species.	957	III	O	*1.4*	1.0	*0.8*	*2.0*	1.7	*1.3*		
XXII. Opuntiales.											
82. Cactaceae.											
Cereus giganteus Engelm.	J401	IV	M	*0.7*	0.5	*0.4*	*1.1*	0.8	*0.5*		
Opuntia echinocarpa Engelm. & Bigel.	J402	IV	M	*0.2*	0.1	*0.1*	*0.5*	0.4	*0.3*		
XXIII. Myrtiflorae.											
83. Thymelaeaceae.											
Aquilaria Agallocha Roxb.	608	IV	O	*0.5*	0.4	*0.3*	*1.1*	0.9	*0.7*		
Wikstroemia sandwichensis Meissn.	920	IV	M	*0.3*	0.2	*0.1*	*0.9*	0.7	*0.4*		
84. Lythraceae.											
Adenaria floribunda H. B. & K.	1601	IV	O	*0.6*	0.3	*0.2*	*1.0*	0.8	*0.6*		
Lafoensia punicaefolia DC.	1600	IV	M	*0.5*	0.5	*0.4*	*1.5*	1.0	*0.7*		
Lagerstroemia reginae Roxb.	847	IV	M	*0.5*	0.4	*0.3*	*1.5*	1.2	*0.6*		
85. Sonneratiaceae.											
Sonneratia acida Linn.	904	IV	O	*0.8*	0.5	*0.2*	*1.2*	1.0	*0.6*	0.3	0.4
86. Lecythidaceae.											
Barringtonia species.	280	IV	O	*0.7*	0.5	*0.3*	*2.0*	1.6	*1.0*		
Eschweilera species.	1620	IV	M	*0.7*	0.5	*0.4*	*1.6*	1.3	*1.1*		
species.	1621	IV	O	*0.6*	0.4	*0.3*	*1.5*	1.3	*0.9*		
87. Rhizophoraceae.											
Bruguiera gymnorrhiza Lam.	548	I	M	*1.2*	1.0	*0.7*	*2.1*	1.7	*1.3*		
Carallia integerrima DC.	550	III	O	*1.3*	1.1	*0.8*	*3.1*	2.6	*2.2*		
Cassipourea elliptica Poir.	1585	II	O	*1.5*	1.0	*0.8*	*2.0*	1.6	*1.2*		
Rhizophora Mangle Linn.	J118	I	O	*1.1*	0.8	*0.5*	*1.7*	1.4	*0.9*		
88. Nyssaceae.											
Nyssa aquatica Linn.	J419	I	M	*1.4*	1.1	*0.7*	*1.7*	1.4	*1.2*	0.7	1.0

TABLE II — *Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
89. Alangiaceae.											
Alangium Lamarckii Thw.	89	III	O	*0.8*	0.6	*0.4*	*1.7*	1.5	*1.2*		
90. Combretaceae.											
Anogeissus latifolia Wall.	846	IV	O	*0.6*	0.4	*0.3*	*1.6*	1.3	*1.1*	0.2	0.4
Lumnitzera littorea Voigt.	61	III	M	*0.8*	0.5	*0.3*	*1.8*	1.5	*0.9*		
Terminalia alata D. Dietr.	873	IV	O	*0.6*	0.4	*0.2*	*1.6*	1.1	*0.9*		
edulis F. Muell.	68	III	M	*0.7*	0.5	*0.4*	*1.6*	1.3	*0.9*		
91. Myrtaceae.											
Eucalyptus rostrata Schlecht.	378	IV	M	*0.4*	0.3	*0.2*	*0.8*	0.7	*0.5*	0.3	0.4
Eugenia perpallida Merrill.	410	IV	M	*1.0*	0.6	*0.3*	*1.8*	1.5	*1.1*		
Metrosideros polymorpha Gaudich.	927	IV	M	*1.0*	0.8	*0.5*	*2.0*	1.7	*1.2*		
92. Melastomataceae.											
Memecylon edule Roxb.	486	IV	M	*0.4*	0.3	*0.2*	*1.1*	0.8	*0.7*		
Miconia species.	1609	IV	M	*0.7*	0.5	*0.3*	*0.8*	0.6	*0.3*		
Tibouchina mutabilis Cogn.	1612	IV	M	*0.6*	0.5	*0.4*	*1.0*	0.8	*0.6*		
93. Oenotheraceae.											
Fuchsia excorticata Linn. f.	495	IV	M	*0.4*	0.3	*0.2*	*0.9*	0.7	*0.4*		
XXIV. Umbelliflorae.											
94. Araliaceae.											
Aralia spinosa Linn.	J683	IV	M	*0.6*	0.4	*0.2*	*1.0*	0.7	*0.5*	0.4	0.5

Cheirodendron Gaudichaudii Seem.	947	II	M	*1.5*	1.2	*0.8*	*1.6*	1.4	*1.0*	0.6	0.8
platyphylla Seem.	917	II	M	*1.1*	1.0	*0.6*	*1.6*	1.3	*1.0*	0.6	0.7
Polyscias nodosa Seem.	30	II	O	*1.1*	1.0	*0.7*	*1.4*	1.3	*1.0*	0.6	0.8
95. Cornaceae.											
Cornus florida Linn.	J412	I	O	*1.4*	1.1	*0.8*	*2.0*	1.7	*1.4*	0.6	0.8
Corokia Cotoneaster Raoul.	97	I	M	*1.3*	0.7	*0.4*	*0.9*	0.8	*0.7*		
Daphniphyllopsis capitata Kurz.	862	I	O	*2.2*	1.7	*1.1*	*3.1*	2.6	*1.7*		
Griselinia lucida Forst. f.	98	I	M	*2.2*	1.9	*1.6*	*2.3*	2.1	*1.6*		
B. METACHLAMYDEAE.											
XXV. Ericales.											
96. Clethraceae.											
Clethra alnifolia Linn.	801	I	Y	*1.1*	0.8	*0.5*	*1.1*	0.9	*0.7*		
97. Ericaceae.											
Andromeda ferruginea Walt.	J427	I	O	*1.0*	0.8	*0.6*	*1.4*	1.1	*0.9*		
Arbutus Menziesii Pursh.	J423	II	O	*0.7*	0.5	*0.4*	*0.9*	0.7	*0.5*		
Arctostaphylos tomentosa Lindl.	J437	II	M	*0.5*	0.4	*0.2*	*0.7*	0.6	*0.4*		
Kalmia latifolia Linn.	J430	I	O	*0.9*	0.8	*0.7*	*1.1*	1.0	*0.8*	0.4	0.5
Oxydendrum arboreum DC.	J429	II	O	*0.7*	0.5	*0.4*	*1.1*	0.9	*0.7*		
Rhododendron catawbiense Michx.	J432	I	O	*0.5*	0.4	*0.2*	*0.7*	0.5	*0.4*		
Vaccinium arboreum Marsh.	J420	I	O	*0.5*	0.4	*0.3*	*0.9*	0.7	*0.6*		
corymbosum Linn.	J421	II	O	*0.6*	0.4	*0.3*	*0.9*	0.8	*0.6*		
98. Epacridaceae.											
Dracophyllum latifolium A. Cunn.	1450	I	Y	*0.6*	0.4	*0.2*	*0.8*	0.5	*0.3*	0.4	0.5
XXVI. Primulales.											
99. Myrsinaceae.											
Ardisia Pickeringia Torr. & Gray.	J439	IV	O	*0.5*	0.4	*0.3*	*1.1*	0.9	*0.7*	0.3	0.4
Myrsine Rapanea Roem. & Schult.	J441	IV	M	*0.7*	0.5	*0.4*	*1.2*	0.9	*0.7*		
Suttonia Lessertiana Mez.	933	IV	M	*0.6*	0.5	*0.4*	*1.1*	0.8	*0.5*		
XXVII. Ebenales.											
100. Sapotaceae.											
Bumelia cuneata Sw.	J445	IV	M	*0.4*	0.3	*0.2*	*1.6*	1.3	*1.1*	0.3	0.6

TABLE II — *Continued.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
Illipe Betis Merrill.	571	IV	M	*1.0*	0.6	*0.4*	*1.5*	1.3	*1.1*		
Palaquium luzoniense Vidal.	577	III	M	*1.4*	1.2	*0.7*	*2.6*	1.9	*1.2*	0.7	0.9
philippense C. B. Robinson.	576	III	O	*1.1*	0.8	*0.6*	*1.8*	1.5	*1.1*		
Sideroxylon species.	924	III	O	*0.8*	0.7	*0.6*	*1.5*	1.3	*1.1*		
101. Ebenaceae.											
Diospyros philippinensis A. DC.	137	IV	O	*0.5*	0.4	*0.3*	*1.0*	0.9	*0.7*		
virginiana Linn.	J452	IV	O	*0.5*	0.4	*0.3*	*1.3*	1.0	*0.8*	0.4	0.6
Maba sandwicensis A. DC.	905	IV	M	*0.4*	0.3	*0.2*	*1.1*	1.0	*0.8*		
102. Symplocaceae.											
Symplocos tinctoria L'Hérit.	J97	I	O	*1.4*	1.1	*0.6*	*2.2*	1.6	*1.2*	0.5	0.8
103. Styracaceae.											
Halesia diptera Linn.	J454	I	M	*1.1*	0.9	*0.8*	*2.3*	1.6	*1.3*	0.7	0.9
XXVIII. Contortae.											
104. Oleaceae.											
Fraxinus americana Linn.	J456	IV	O	*0.4*	0.3	*0.2*	*1.2*	0.8	*0.7*	0.2	0.6
Olea lanceolata Hook. f.	492	III	Y	*0.6*	0.4	*0.3*	*1.4*	1.2	*0.9*		
Schrebera swietenioides Roxb.	493	III	O	*0.5*	0.4	*0.3*	*1.6*	1.4	*0.8*		
105. Loganiaceae.											
Fagraea fragrans Roxb.	362	IV	O	*0.6*	0.5	*0.4*	*1.6*	1.3	*1.0*		

Geniostoma ligustrifolium A. Cunn.	363	III	O	*0.7*	0.6	*0.4*	*1.0*	0.9	*0.6*	0.5	0.8
Strychnos species.	364	IV	O	*0.7*	0.5	*0.4*	*2.1*	1.7	*1.2*		
106. Apocynaceae.											
Alstonia macrophylla Wall.	100	IV	O	*1.1*	0.9	*0.6*	*2.0*	1.5	*1.0*		
Rauwolfia sandwicensis A. DC.	976	III	M	*1.2*	1.0	*0.8*	*1.9*	1.6	*1.1*	0.5	0.8
Wrightia tinctoria R. Br.	N1115	IV	M	*0.5*	0.3	*0.2*	*1.0*	0.8	*0.6*		
107. Asclepiadaceae.											
Asclepias species.	1094	IV	M	*0.2*	0.2	*0.1*	*0.8*	0.6	*0.4*		
XXIX. Tubiflorae.											
108. Hydrophyllaceae.											
Eriodictyon tomentosum Benth.	1004	III	Y	*0.6*	0.5	*0.3*	*1.0*	0.8	*0.7*		
109. Borraginaceae.											
Bourreria havanensis Miers.	J471	IV	M	*0.5*	0.3	*0.2*	*1.1*	0.9	*0.6*	0.3	0.6
Cordia Gerascanthus Linn.	1619	IV	M	*0.4*	0.3	*0.2*	*2.0*	1.7	*1.4*		
Ehretia Wallichiana Hook. f. & Thoms.	941	III	O	*0.6*	0.5	*0.4*	*2.4*	1.9	*1.0*		
110. Verbenaceae.											
Avicennia officinalis Linn.	632	IV	M	*0.3*	0.2	*0.2*	*1.4*	1.2	*1.0*	0.2	0.4
Premna longifolia Roxb.	1054	IV	O	*0.9*	0.5	*0.3*	*1.4*	1.2	*1.0*		
Vitex Aherniana Merrill.	624	IV	O	*0.6*	0.5	*0.4*	*1.7*	1.4	*1.1*		
111. Solanaceae.											
Nicotiana glauca R. Grah.	855	IV	M	*0.4*	0.3	*0.2*	*1.0*	0.9	*0.6*		
Solanum auriculatum Ait.	1462	IV	M	*0.5*	0.3	*0.2*	*0.8*	0.7	*0.5*		
sandwicense Hook. & Arn.	948	IV	M	*0.4*	0.3	*0.2*	*1.1*	0.8	*0.5*		
112. Scrophulariaceae.											
Paulownia imperialis Sieb. & Zucc.	579	IV	M	*0.4*	0.3	*0.2*	*1.2*	0.9	*0.6*		
113. Bignoniaceae.											
Catalpa speciosa Warder.	J476	IV	O	*0.4*	0.3	*0.2*	*1.0*	0.8	*0.5*	0.1	0.3
Tabebuia pentaphylla Hemsl.	1603	IV	M	*0.4*	0.3	*0.2*	*1.1*	0.9	*0.7*		
114. Gesneriaceae.											
Rhabdothamnus Solandri A. Cunn.	1172	III	Y	*0.6*	0.5	*0.2*	*0.8*	0.7	*0.4*		

TABLE II — *Concluded.*

Designation		Older Wood								First Annual Ring	
		Type	Age	Vessel Segments			Other tracheary cells			Vessel segments	Other tracheary cells
Plant	No.			Max.	Mean	Min.	Max.	Mean	Min.	Mean	Mean
115. Myoporaceae.											
Myoporum laetum Forst.	488	IV	M	*0.5*	0.4	*0.3*	*1.5*	1.3	*0.9*		
sandwicense A. Gray.	972	IV	M	*0.6*	0.4	*0.3*	*1.1*	0.9	*0.6*	0.3	0.5
XXX. Rubiales.											
116. Rubiaceae.											
Cephalanthus occidentalis Linn.	J482	IV	M	*0.6*	0.5	*0.4*	*1.1*	0.9	*0.6*		
Nauclea media Havil.	531	IV	M	*1.1*	0.8	*0.6*	*1.8*	1.6	*1.4*		
Straussia hawaiensis A. Gray.	988	III	M	*0.8*	0.5	*0.4*	*1.1*	0.9	*0.6*	0.4	0.5
117. Caprifoliaceae.											
Lonicera involucrata Banks.	J512	III	M	*0.6*	0.5	*0.4*	*1.1*	0.8	*0.7*	0.4	0.7
Sambucus nigra Linn.	J489	III	M	*0.4*	0.3	*0.2*	*1.3*	1.1	*0.9*	0.3	0.5
Viburnum Lentago Linn.	J491	I	O	*1.2*	1.0	*0.8*	*1.8*	1.5	*1.2*		
XXXI. Campanulatae.											
118. Compositae.											
Baccharis halimifolia Linn.	J501	IV	M	*0.2*	0.2	*0.1*	*0.7*	0.5	*0.3*	0.2	0.3
Dubautia plantaginea Gaudich.	946	IV	M	*0.4*	0.3	*0.2*	*0.9*	0.7	*0.6*		
Perymenium species.	1564	IV	M	*0.4*	0.3	*0.2*	*1.1*	0.9	*0.7*		
Vernonia species.	1046	IV	M	*0.3*	0.2	*0.1*	*0.4*	0.3	*0.2*		

The most salient features of these tables are the following: (1) There is a marked contrast in length between the innermost or first formed and subsequently formed tracheary elements of the secondary xylem. In Ginkgo and the Coniferae, the latter are from 200–600 percent longer than the former. There is a similar, though less pronounced, contrast in size between the innermost and outermost tracheids, fiber-tracheids and libriform fibers of the secondary xylem of dicotyledons. (2) The vessel-segments of the dicotyledons are invariably somewhat shorter than the surrounding tracheary elements of the secondary xylem; but in certain stems, the vessel-segments of the first formed growth layers are of the same length as those which occur in the later formed wood. (3) Although extremely variable in size, the tracheids of Gymnosperms are, on an average, noticeably longer than equivalent tracheary elements of dicotyledons, Table III. This contrast in size is somewhat less conspicuous in the case of the tracheary elements of the first formed secondary xylem. (4) In the dicotyledons, the fiber-like tracheary elements tend to become shorter as the vessel-segments decrease in length, Table III. (5) In the dicotyledons, there is no close correlation between the size of the tracheary elements and the various types of floral organization which form the basis of the Engler and Gilg (1912) system of classification. (6) In the Coniferae, the tracheary elements of the Taxaceae and Cupresseae average somewhat shorter, and those of the Taxodieae and Araucarieae somewhat longer, than the tracheids of the Abieteae, Table III.

Sanio (1872) came to the conclusion that in the stems and branches of *Pinus sylvestris* Linn. the tracheids everywhere increase from within outwards, throughout a number of annual rings, until they have attained a definite size, which then remains constant for the following annual rings.[5] Shepard and Bailey (1914) and subsequently Miss Gerry (1915) and Lee and Smith (1916) have shown that Sanio's law is not applicable to conifers in general. In *Pinus Strobus* Linn., *P. palustris* Mill., *Picea rubens* Sarg., *Pseudotsuga taxifolia* Britton, *Tsuga canadensis* Carr., and *Abies concolor* Lindl. and Gord., the tracheids were found to increase rapidly in length for a period of years, varying from 20–60; but no constant length was attained even in trees several hundred years old. Following the first period of rapid increase in length the size of the tracheids fluctuated more or less during the subsequent growth of the plant. Similar results have been

5 Sanio's constants occurred after 18–40 years.

TABLE III.

GYMNOSPERMAE — DICOTYLEDONEAE.

SECONDARY XYLEM OF STEM.

Frequency distribution of average lengths of tracheary elements.

Designation	No. Ind.	Class Centers									
		.2	.5	.8	1.1	1.4	1.7	2.0	2.3	2.6	2.9
Gymnosperms: Outer Tracheids	152	....	....	....	....	1	4	12	10	19	13
" Inner "	48	....	5	27	13	3	....	....	....	....	....
Dicotyls: Outer "Fibers"	275	4	26	66	66	53	35	13	3	4	4
" Inner "	81	5	37	26	10	2	1	....	....	....	....
" Outer Vessel-segments	275	76	104	49	29	7	7	3	....	....	....
" Inner "	81	35	26	19	...	1	....	....	....	....	....
Araucarieae: Outer Tracheids.	6	....	....	....	....	....	....	....	....	....	....
Taxodieae: " "	10	....	....	....	....	....	....	....	....	1	1
Abieteae: " "	88	....	....	....	....	....	1	5	4	10	11
Taxaceae: " "	15	....	....	....	....	....	1	3	2	3	....
Cupresseae: " "	27	....	....	....	....	1	2	4	4	5	1
Dicotyls I: Outer "Fibers"	53	....	3	4	9	9	12	6	2	3	4
" I: Inner "	28	....	4	13	8	2	1	....	....	....	....
" IV: Outer "	169	4	21	50	48	29	13	4	....	....	....
" IV: Inner "	36	5	27	4	....	....	....	....	....	....	....
" I: Outer Vessel-segments	53	1	3	17	15	7	7	3	....	....	....
" I: Inner "	28	....	11	16	....	1	....	....	....	....	....
" IV: Outer "	169	74	79	16	....	....	....	....	....	....	....
" IV: Inner "	36	32	4	....	....	....	....	....	....	....	....

TABLE III (*Continued*).

in Millimeters.														Statistical Constants	
3.2	3.5	3.8	4.1	4.4	4.7	5.0	5.3	5.6	5.9	6.2	6.5	6.8	7.1	Mean in. mm.	S D in mm.
23	12	11	5	12	6	7	7	2	0	1	5	1	1	3.53± .07	1.25± .05
....	....	....	....	(C)	....	....	....	(C)	....	....	....	....	....	.90± .02	.25± .02
1	....	....	....	(V)	....	....	....	....	....	....	....	....	....	1.20± .02	50± .01
....	....	....	....	....	....	....	....	....	....	....	....	....	....	.69± .02	.28± 01
....	....	....	....	....	....	....	....	....	....	....	....	....	....	.61± .02	.41± .01
....	....	....	....	....	....	....	....	....	....	....	....	....	....	.45± .02	.26± .01
....	1	....	....	....	....	....	1	....	....	1	2	....	1	5.85± .32	1.18± .23
1	....	....	1	....	1	1	....	1	....	....	3	....	....	4.76± .31	1.44± .22
16	7	6	4	12	4	3	4	1	....	....	....	....	....	3.49± .07	.92± .05
3	....	2	....	....	....	1	....	....	....	....	....	....	....	2.82± .15	.86± .11
3	3	3	....	....	1	....	....	....	....	....	....	....	....	2.74± .10	.77± .07
1	....	....	....	....	....	....	....	....	....	....	....	....	....	1.64± .06	.67± .04
....	....	....	....	....	....	....	....	....	....	....	....	....	....	.92± .04	.28± .03
....	....	....	....	....	....	....	....	....	....	....	....	....	....	1.04± .02	.37± .01
....	....	....	....	....	....	....	....	....	....	....	....	....	....	.49± .02	.14± .01
....	....	....	....	....	....	....	....	....	....	....	....	....	....	1.12± .04	.41± .03
....	....	....	....	....	....	....	....	....	....	....	....	....	....	.70± .02	.17± .02
..	....	....	....	....	....	....	....	....	....	....	....	....	....	.40± .01	.20± .01
....	...	...	....	....	....	....	....	....	....	....	....	....	....	.24± .01	.10± .01

C — Cycads. V — Vesselless Dicotyls.

secured by the writers, *Figs. 1, 3,* and *4*. It seems probable, however, from the study of available data, that, although in most cases the length of the tracheids does not become constant in the older wood of individual stems of coniferous plants, the normal length-on-age curve for any particular species is of the general form illustrated in *Graph 16, Fig. 5*.

In any given plant, the length-on-age curve, or one or more portions of it, may deviate from the norm of the species, owing, in all probability, to the effects of various environmental factors. Thus, stunted or depauperate plants appear to have depressed curves, *Graphs 12, 12a, 5a, 5b, 14, 14a,* and *8*. Furthermore, the distorted tracheary tissue, formed subsequent to injury or in response to abnormal growth conditions, frequently possesses shorter tracheids than normal tissue, *A, Graphs 13* and *5a*. Similarly, tissue formed in regions of the plant where there are considerable mechanical stresses, e. g. at the junction of stems and roots or stems and branches or in bent or twisted stems, tends to have shorter tracheids than normal straight grained tissue. This is shown very clearly in the following table:

TABLE IV.

Pinus Strobus.

Stems one year old.

	Length tracheids mm.
Specimen No. 1.	
Wood from vicinity of branch whorl	0.43
Wood from stem between branch whorls	0.82
Specimen No. 2.	
Wood from vicinity of branch whorl	0.62
Wood from stem between branch whorls	0.96
Specimen No. 3.	
Wood from vicinity of branch whorl	0.65
Wood from stem between branch whorls	0.84
Specimen No. 4.	
Wood from vicinity of branch whorl	0.65
Wood from stem between branch whorls	0.99
Specimen No. 5.	
Wood from vicinity of branch whorl	0.71
Wood from stem between branch whorls	1.16

	Length tracheids mm.
Stems 25 years old	
Wood from vicinity of branch whorl	
First annual ring	0.6
10th " "	1.9
25th " "	2.2
Wood 6 inches from whorl	
First annual ring	0.9
10th " "	2.3
25th " "	3.6
Wood 12 inches from whorl	
First annual ring	1.0
10th " "	2.4
25th " "	3.8

Furthermore, Hartig (1901) and Shepard and Bailey (1914) have shown that the peculiar compression wood (*Rothholz*) which occurs on the under sides of branches and on the concave sides of bent stems is composed of shorter tracheids than the tension wood (*Zugholz*) which occurs on the opposite sides of the same branches or stems.

In view of these facts, the longest tracheids might be expected to occur in the old, straight grained wood of the "clear length" of the stem, or that portion between the swollen base and crown which is devoid of large branches. That longer tracheids do actually occur in this portion of the stem, is indicated by the measurements of Sanio (1872), Shepard and Bailey (1914) and Lee and Smith (1916), and is graphically shown in *Figs. 4* and *5*. *Graphs 17* and *17a* are of considerable interest in this connection. The secondary tracheids near the pith are of similar lengths at distances of from 2–154 feet above the level of the ground. On the other hand, the average length of the tracheids in the older wood — last 60–100 annual rings — is considerably less in the 2–26 and 138–154 foot sections of the stem. In other words, it seems probable that as a plant becomes older, the depressing effect of the conditions at the base of the plant extends further and further up the stem, and persistent branches have a progressively greater influence upon the surrounding tissue of the main axis of the plants. Therefore, in certain sections removed from the bases and tops of large trees, it is not uncommon to find that the tracheary elements — after increasing in length for a period of years — tend to become shorter in the outermost rings of the stem; a phenomenon which might easily be mistaken for senility, *Graph 5b*, *Fig. 3*.

It is evident, accordingly, that the means in Table I cannot be considered *a priori*, as the tracheary size norms of the species listed. However, in view of the varied character of the material studied, the table as a whole may be considered to give a fairly reliable indication of the general size (length) variations that occur in the tracheary elements of the stems of Coniferae. Long tracheids tend to occur in the "clear lengths" of the stems of tall, rapidly growing forest trees; short tracheids in xerophytes, small, slowly growing or depauperate individuals, and plants whose stems are clothed nearly to the level of the

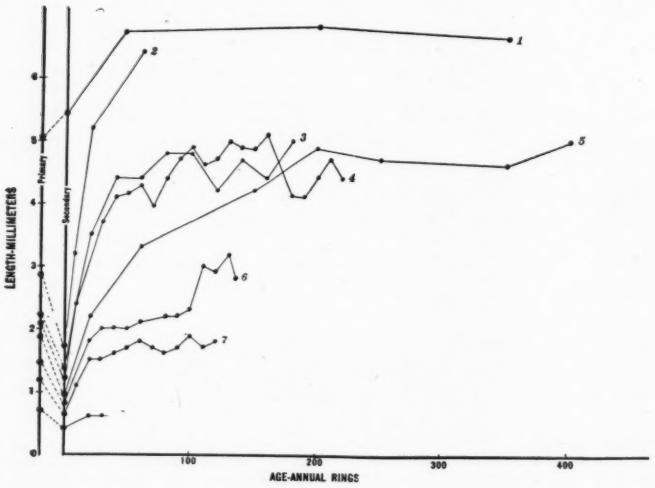

FIGURE 1. Graphs illustrating variation in length of tracheids in passing from the innermost to the outermost secondary xylem. Lengths of primary tracheids shown for comparison. 1. *Dioon spinulosum;* 2. *Araucaria Bidwillii;* 3. *Pseudotsuga taxifolia,* after Lee and Smith; 4. *Pinus palustris;* after Shepard and Bailey; 5. *Pinus ponderosa,* 6. *Cedrus Libani;* 7. *Taxus brevi folia;* 8. *Pinus albicaulis.*

ground, with large persistent branches. In Table III, the proportion of the former types of growth forms is higher in the Taxodieae and Abieteae than in the Taxaceae and Cupresseae.

It has been shown in Table II that, in the stems of dicotyledons, the first formed tracheids, fiber-tracheids and libriform fibers tend to

be considerably shorter than the later formed elements of the secondary xylem. The segments of vessels are usually somewhat shorter in the first formed than the older secondary xylem, although this is not invariably the case, particularly in plants listed as of Group IV. In this group, relatively short vessel-segments may be of the same length in the innermost and outermost parts of the secondary xylem, a phenomenon noted by Sanio (1873–74) in certain Leguminosae.

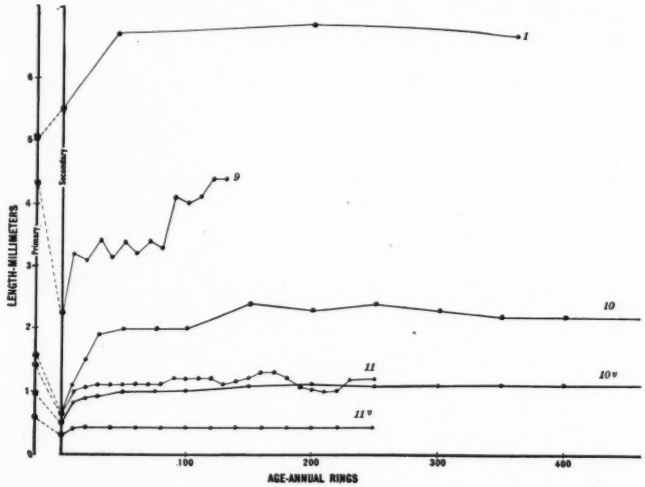

FIGURE 2. Graphs illustrating variation in length of tracheary elements in passing from innermost to outermost secondary xylem. Lengths of primary elements shown for comparison. 1. *Dioon spinulosum;* 9. *Trochodendron aralioides,* vesselless arborescent dicotyledon, stunted specimen; 10. *Liriodendron tulipifera,* fiber-tracheids; 10v. *Same,* vessel-segments; 11. *Carya ovata,* fiber-tracheids after Pritchard and Bailey; 11v. *Same,* vessel-segments after Pritchard and Bailey.

As is indicated in *Figs. 2* and *4*, *Graphs 10, 10v, 11, 11v, 15* and *15v,* the tracheary elements in the first formed growth layers of most arborescent and fruticose dicotyledons become progressively longer for a period of from 5–20 years. During succeeding growth in diameter of the stem, the length of the elements remain nearly constant or fluctuate more or less, apparently in response to environmental influences. Injuries or other abnormal growth conditions tend to cause

the formation of shorter tracheary elements, *A Fig. 4, Graphs 15* and *15v.* Similarly, the size of the tracheary cells tends to be less in nodes, junctions of stems and roots or branches and other regions where growth adjustments are taking place, Table V.

TABLE V.

	Node	*Internode*
Trochodendron aralioides		
Tracheids of first two rings	1.4 mm.	1.9 mm.
Carya ovata		
Fiber-tracheids of first two rings	0.5 mm.	0.6 mm.
Vessel-segments " " " "	0.2 mm.	0.3 mm.
	Stump	*"clear length"*
Betula lutea		
Fiber-tracheids of mature wood	1.2 mm.	1.7 mm.
Vessel-segments " " "	0.7 mm.	1.2 mm.

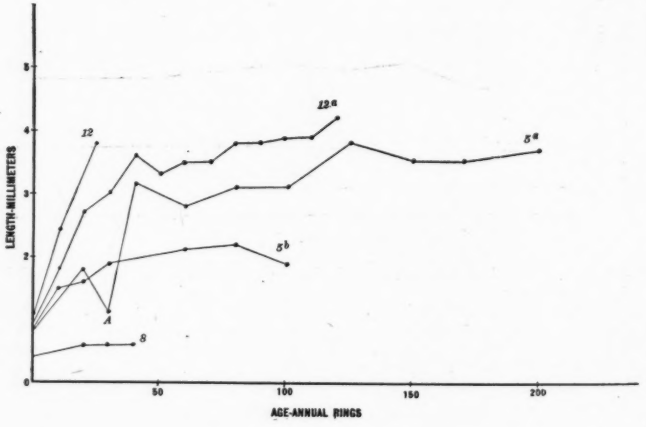

FIGURE 3. Graphs illustrating effects of environmental factors on lengths of tracheids. 12. *Pinus Strobus*, vigorous, rapidly grown specimen; 12a. *Same*, plant suppressed during first 60 years; 5a. *Pinus ponderosa*, effects of injury at A; 5b. *Same*, stunted specimen, 12 feet high at 100 years; 8. *Pinus albicaulis*, alpine plant, one foot high at 45 years.

Therefore, longer tracheary elements tend to occur in the "clear lengths" of the stems of tall, vigorous, rapidly growing forest trees,

and shorter cells in small or depauperate plants, and stems which are covered with large persistent branches. However, the size of the tracheary elements varies considerably even in dicotyledons of similar growth forms. These fluctuations appear to be concomitants of certain structural changes in the xylem.

It was shown by von Mohl (1851) in the middle of the last century that vessels are compound structures which arise from series of cells by the loss of the pit membranes in the division walls between the members of the series. In certain types of secondary xylems, the vessel-segments closely resemble scalariform tracheids in general form

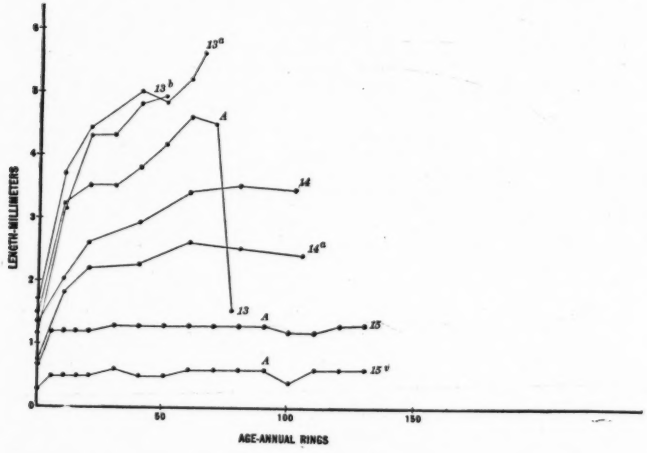

FIGURE 4. Graphs illustrating the effects of environmental factors on the length of tracheary elements. 13. *Pinus Taeda*, section 1½ feet from ground, effects of injury at A; 13a. *Same*, section 32 feet from ground; 13b. *Same*, section 62 feet from ground; 14. *Pinus contorta* var. *Murrayana*, vigorous specimen; 14a. *Same*, stunted specimen; 15. *Swietenia Mahogoni*, libriform fibers, effects of injury at A; 15v. *Same*, vessel-segments, effects of injury at A.

and structure, *Fig. 6*. In these presumably more primitive types of vessels certain of the pits in the end walls of the individual tracheary cells have no pit membranes and are without well marked bordering areas of the secondary walls. These types of vessels grade into others in which the scalariform openings become larger and reduced in number and coalesce to form single large openings or pores. At the same

time the constituent cells of the vessels become wider and their ends tend to become less tapering. The most specialized condition results in the formation of tubes of relatively large bore which are composed of wide segments with nearly horizontal end walls.

In Table II, four categories of vessels have been recognized. In group I, the perforations are prevailing scalariform; in group II, intermediate between scalariform and porous; and in groups III and

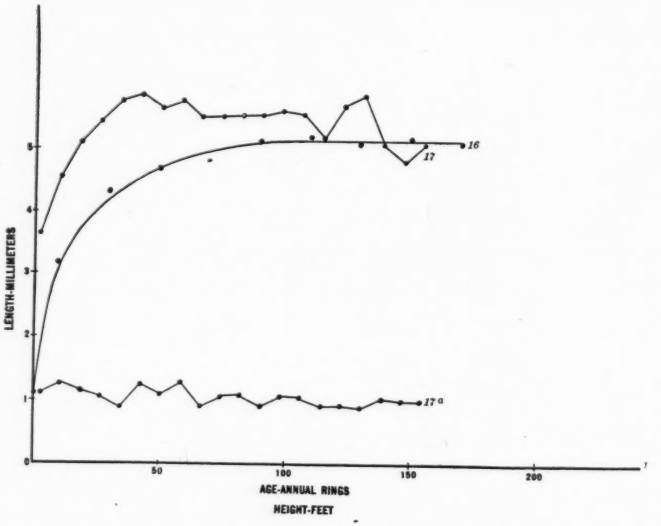

FIGURE 5. Graph 16. *Pseudotsuga taxifolia*, average length-on-age curve, for eight sections removed from different trees and at different heights; 17. *Same*, average lengths of tracheids in outer rings of a large stem, at heights of from 2–154 feet above the level of the ground; 17a. *Same*, Length of tracheids in first annual ring, at heights of from 2–154 feet above the level of the ground.

IV, prevailing porous *Fig. 6*. The vessel-segments in group III differ from those in group IV in having well marked tapering ends, thus resembling tracheids in general outline.

That tracheary elements tend to shorten as vessels become more highly differentiated is indicated by the data in Tables II and III. If the material in the various groups were made strictly comparable, it would tend to accentuate the differences between the lengths of the

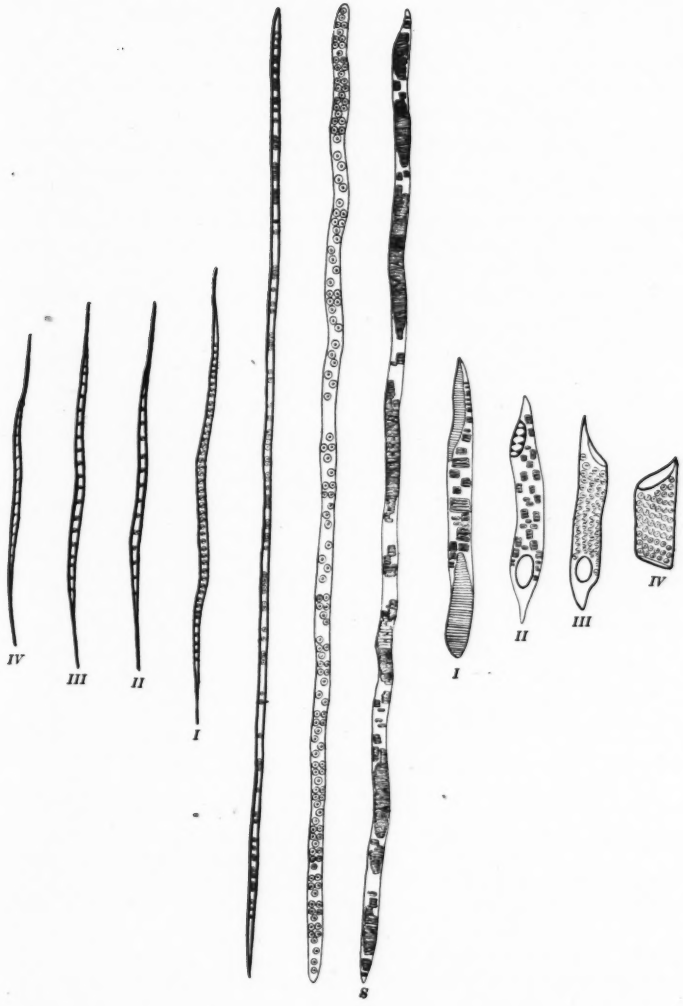

FIGURE 6. Diagrammatic illustration of average size and structure of tracheary elements in the mature wood of Coniferae and various groups of Dicotyledoneae, based upon measurements in Tables I and II. S. Scalariform tracheid of Trochodendron or Dioon, not drawn to scale.

elements in groups I and IV. For example, in groups I and II, 12 percent of the specimens are less than 15 years old, whereas in groups III and IV 5 percent are less than 15 years old.

It is evident, accordingly, that there is an important correlation between the size of tracheary elements in arborescent and fruticose Dicotyledons and certain types of differentiation of the secondary xylem. As the vessels become wider and more highly specialized structually, the tracheary elements tend to become shorter. Not only do the elements tend to become shorter, but the bordered pits in their lateral walls become correspondingly modified, Table VI.

TABLE VI.

Angiospermae — Dicotyledoneae.

Types of lateral pitting.

Group I	Vessel-segments:	Scalariform and opposite	86%
"	" " :	Opposite and alternate or alternate	14%
"	Other tracheary cells:	Medium or large borders	63%
"	" " " :	Small borders	20%
"	" " " :	Borders vestigial or absent	17%
Group II	Vessel-segments:	Scalariform and opposite	80%
"	" " :	Opposite and alternate or alternate	20%
"	Other tracheary cells:	Medium or large borders	35%
"	" " " :	Small borders	30%
"	" " " :	Borders vestigial or absent	35%
Group III	Vessel-segments:	Scalariform and opposite	11%
"	" " :	Opposite and alternate or alternate	89%
"	Other tracheary cells:	Medium or large borders	07%
"	" " " :	Small borders	33%
"	" " " :	Borders vestigial or absent	60%
Group IV	Vessel-segments:	Scalariform and opposite	06%
"	" " :	Opposite and alternate or alternate	94%
"	Other tracheary cells:	Medium or large borders	05%
"	" " " :	Small borders	12%
"	" " " :	Borders vestigial or absent	83%

In groups III and IV, alternate-multiseriate pitting predominates in the lateral walls of the vessels, whereas, in groups I and II, scalariform and opposite-multiseriate pitting are much in evidence. The tracheary elements which surround the vessels in groups I and II usually have conspicuous bordering areas about the pit orifaces in

their lateral secondary walls, but this is not the case in groups III and IV. In other words, with increasing specialization certain tracheary cells become highly modified and serve principally as conductors of liquids, whereas others gradually cease to serve in that capacity, and become modified as mechanical or skeletal elements, *Fig. 6*. Each line of specialization appears to involve a general tendency towards reduction in the length of the tracheary elements and concomitant changes in the structure and arrangement of the pits.

Furthermore, as the secondary xylem becomes more and more highly differentiated, the contrast in length — in the later formed growth layers — between vessel-segments and surrounding tracheary elements usually becomes correspondingly accentuated.

The fact that vessel-segments are shorter than the tracheids, fiber-tracheids or libriform fibers which surround them, and that, in the dicotyledons, the tracheary elements become shorter as the vessels become more highly differentiated, suggests that the striking general contrast in cell length between the secondary tracheary elements of the gymnosperms and dicotyledons may be closely correlated with the evolution of vessels in the later group of plants. That the reduced size (length) of the tracheary elements in the dicotyledons is associated in some way with the development of vessels is emphasized, furthermore, by the fact that such vesselless arborescent plants as Trochodendron and Drimys have the longest tracheary elements of any of the dicotyledons investigated, *Table VII*. In addition it is significant that the tracheary elements of the secondary xylem of the Gnetales, supposed gymnosperms with vessels, resemble in length those that occur in many dicotyledons, *Table VII*.

TABLE VII.

Vesselless Angiosperms.		
Trochodendron aralioides Sieb. & Zucc.	Tracheids	4.5 mm.
Drimys Winteri Forst.	"	4.3 mm.
Gnetales.		
Ephedra californica S. Wats.	Vessel-segments	0.7 mm.
	Tracheids	0.8 mm.
Gnetum Gnemon Linn.	Vessel-segments	1.5 mm.
	Tracheids	1.9 mm.
Welwitschia mirabilis Hook. f.	Vessel-segments	0.7 mm.

Size of tracheary Elements in vascular Cryptogams and older Gymnosperms.

The tracheids in the vascular cryptogams appear to have been of such unusual length as to attract the attention of many paleontologists. The great length of the secondary tracheids in Calamites led Williamson (1871) to describe them as vessels — compound structures — in one of his earlier papers. Williamson and Scott (1894) described the tracheary elements of Sphenophyllum as follows: "If they were tracheids they must have been of great length, for they can often be traced all through a section without finding any terminal wall." In another paper, these writers (1895) stated that in Lyginodendron the secondary "tracheids are of great length" and that in Heterangium "their length must have been great as terminations are by no means frequently seen." Williamson (1873) had previously stated in regard to the tracheary elements of *Dictyoxylon Oldhamium:* "It is very difficult to measure their length, because, owing to its amount which is considerable, and to their interlacing freely within their respective bundles, it is almost impossible to see the extremities of each fiber; it is, however, sufficiently great to give them an almost vascular character." Similar descriptions have been recorded by other paleontologists.

Through the courtesy of Drs. G. R. Wieland and E. W. Berry, the writers secured the opportunity of examining sections of well preserved fossil stems of various representatives of the Calamariales, Sphenophyllales, Lepidophytineae and Cycadofilices, and of verifying the statements of previous investigators. The tracheary elements of the secondary xylem in such forms as Calamites, Sphenophyllum, Lepidodendron, Sigillaria, Lyginodendron, Heterangium and other Cycadofilices were undoubtedly very long, averaging usually several millimeters. The first formed secondary tracheids appear to have been as long if not longer than the primary tracheids, but the tracheids of nodal wood — at least in the Calamariales — were apparently somewhat shorter than those of the internodal wood.

The secondary tracheary elements in living representatives of the Cycadales, and in fossil stems of Bennettitales and Cordaitales, resemble in length the tracheids of the vascular cryptogams mentioned above. Although the later formed secondary tracheids may be somewhat longer than those formed by the first activity of the cambium, the latter — in contrast to similar elements of Ginkgo, the Coniferae

and Dicotyledoneae — frequently appear to be relatively long and of nearly the same length, if not actually longer, than the outermost elements of the primary wood, *Graph 1, Fig. 1.* This is in marked contrast to the conditions which occur in the rest of the gymnosperms and woody dicotyledons, in which the primary tracheary elements average as a rule considerably longer than the innermost elements of the secondary xylem, *Figs. 1* and *2.* In other words, the most striking differences in length between the tracheary elements of the higher and lower gymnosperms occur commonly in the innermost cells of the secondary xylem, *Figs. 1* and *2.* Furthermore, whereas, in the older gymnosperms and vascular cryptogams, the secondary xylem of small plants may be composed of relatively long tracheids, the smaller growth forms of the Coniferae tend to have comparatively short tracheids even in the outermost portions of the secondary wood.

Summary.

A comparative study of the secondary xylem of vascular plants reveals a number of interesting facts in regard to the length of the secondary tracheary elements in vascular cryptogams, gymnosperms and angiosperms. The tracheary elements of the secondary xylem in the vascular cryptogams tended to be very long, whereas those which occur in the dicotyledons — with the notable exception of the vesselless Trochodendroceae and Magnoliaceae — are comparatively short. The gymnosperms appear to occupy an intermediate position between these extremes; the Cordaitales, Bennettitales and Cycadales resembling the vascular cryptogams, and the Gnetales — supposed gymnosperms with vessels simulating the angiosperms.

The reduction in the size (length) of the tracheary elements of the higher plants appears to have proceeded along certain general and more or less distinct lines.

(1) In all the dicotyledons and gymnosperms with the exception of the Cordaitales, Bennettitales and Cycadales, the first formed tracheary cells of the secondary xylem are relatively small, and in all of the material examined by the writers are considerably shorter than the adjoining elements of the primary xylem and subsequently formed tracheary cells of the secondary xylem, *Figs. 1* and *2.*[6]

[6] In dicotyledons having very highly differentiated types of vessels, the short vessel-segments may be of nearly uniform size in succeeding growth layers of the secondary xylem.

This is in marked contrast to the conditions which prevailed in the stems of many of the lower vascular plants. In those forms — which possessed relatively wide zones of primary wood — the innermost tracheids of the secondary xylem appear to have resembled in size the elements of the primary xylem. It seems probable, therefore, that in the evolution of the higher gymnosperms and dicotyledons, with reduction in the amount of primary xylem and other changes in the innermost portion of the stele, there has been a concomitant shortening of the first formed tracheary elements of the secondary xylem.

(2) Another tendency towards reduction in the length of the tracheary elements of the secondary xylem appears to be associated with the evolution and differentiation of vessels. The secondary tracheary tissue of the vascular cryptogams and gymnosperms is comparatively simple and composed of cells of a single generalized type, the so-called tracheids. In the evolution of the Gnetales and Dicotyledoneae, specialization or division of labor appears to occur among these cells. Certain vertical series of tracheids become modified and function principally in conducting liquids whereas others become highly modified as mechanical or skeletal elements, *Fig. 6*. That this process of specialization involves a reduction in the length of the tracheary elements, is indicated, not only by the striking general contrasts between the cells of the xylem in the dicotyledons and gymnosperms or vascular cryptogams, but also by the interesting fact that the vesselless Trochodendraceae and Magnoliaceae have very long tracheary elements, and the Gnetales comparatively short ones, such as occur in many dicotyledons. As the vessels of the secondary xylem become more and more highly differentiated their segments gradually lose their resemblance to tracheids, *Fig. 6*, and tend to become progressively wider and shorter. At the same time, the structure and arrangement of the bordered pits in their lateral walls tends to be considerably modified, *Table VI*. Furthermore, the surrounding tracheary elements tend to shorten and to take on a more fiber-like structure, their pits becoming vestigial by the gradual disappearance of the bordering areas of the secondary walls. During these processes of specialization, the reduction in length of the vessel-segments usually exceeds that which occurs in the remaining tracheary elements. That is to say, there is less contrast in length between vessel-segments and surrounding tracheary elements in Group I than in Group II of the dicotyledons.

In addition to these striking tendencies toward reduction in the

length of tracheary elements, there are indications of other variations in cell length which seem to be induced by different factors.

In the Coniferae — among plants of comparable ages — the smaller, slower growing forms, e. g. certain Taxaceae and Cupresseae, tend to have shorter elements than larger, more rapidly growing forms. Furthermore, within the same species, dwarfed or depauperate plants tend to be composed of shorter tracheary elements than normal individuals. Similar tendencies occur among the dicotyledons. It is important to note in this connection, that the tracheary elements formed about the junctions of stems and roots, branches, or leaf traces, wound tissue, compression wood, and similar tissue in which growth adjustments are taking place, tend to be considerably shorter than those which occur in normal internodal or straight grained wood, *Figs. 3, 4,* and *5, Tables IV* and *V*. Of course, the abundance and distribution of this short celled tracheary tissue varies considerably in plants grown in different environments and in plants of different growth habits. Thus, tall forest trees whose stems are devoid of branches over a considerable length of their stem, appear to have longer tracheary cells than non-gregarious trees whose stems are clothed nearly to the level of the ground with large branches. Similarly, gnarled or twisted trees, such as occur commonly in alpine regions and other windswept or exposed situations, have shorter tracheids than erect plants of more sheltered habitats.

In so far as the length of the tracheary elements of the secondary xylem of vascular plants in general is concerned, there is no absolute correlation between body size and cell size. The tracheary elements in large dicotyledons may be considerably smaller than those that occur in comparatively small gymnosperms or vascular cryptogams. Similarly a gigantic sequoia may have shorter cells than a small cycad. Although the secondary tracheary elements in the Coniferae and Dicotyledoneae increase in size as the plants become larger, this phenomenon lasts for only a comparatively limited number of years, after which the size is subject to comparatively slight fluctuations.

It is to be emphasized in conclusion that the primary object of an extensive reconnaissance survey of this character should be to blaze the way for subsequent and more intensive investigations. Having blocked out certain of the more important size variations that occur in the tracheary cells of the secondary xylem of vascular plants, it is essential to isolate and study the factors which regulate or control these phenomena. Of course, the length of the tracheary elements of the secondary xylem is dependent upon (1) the length of the cambial

mother cells which form them and (2) the amount of elongation which they undergo during differentiation. A detailed discussion of the size variations of cambial cells, and the elongation of their daughter cells during differentiation, will be undertaken in the second paper of this series.

ACKNOWLEDGMENTS.

The writers are greatly indebted to Professors R. T. Baker, H. Shirasana, C. J. Chamberlain, O. W. Caldwell, W. P. Thompson, and R. T. Fisher; Messrs. R. D. Swales of the Union Lumber Company, Ralph Staebner of the Little River Lumber Company, R. R. Chaffee of Endeavor, Pa., and H. N. Lee of the Canadian Forest Products Laboratory; and the following members of the U. S. Forest Service (Wm. N. Cluigan, Knower Mills, George Donaldson, Austin Cary, Eloise Gerry, Arthur Koehler, W. D. Brush, R. T. Ferguson, J. B. Connor and Ward Shepard) for their kindness in sending material of various plants, and to Raphael Zou and Bertha Kaplan for assistance with the Russian literature.

BUSSEY INSTITUTION,
Jamaica Plain, Mass.

Literature Cited.

Amelung, E.
1893. Über mittlere Zellengrössen. Flora. 77: 176–207.
Berezowski, A.
1910. Studien über die Zellgrösse. I. Über das Verhältnis zwischen der Zellgrösse und der Gesamtgrösse des wachsenden Organismus. Arch. Zellforsch. 5: 375–384.
Boveri, T.
1904. Ergebnisse über die Konstitution der Chromatischen Substanz des Zellkerns. Jena.
1905. Zellen — Studien. 5. Über die Abhängigkeit der Kerngrösse und Zellenzahl der Seeigel — Larven von der Chromosomenzahl der Ansgangszellen. 1–80. Jena.
Chambers, R.
1908. Einfluss der Eigrösse und der Temperatur auf das Wachstum und die Grösse des Frosches und dessen Zellen. Arch. Mikros. Anat. 72: 607–661.
Conklin, E. G.
1896. Cell size and body size. Abstract in Science. N. S. 3: 59.
1898. Environmental and sexual dimorphism in Crepidula. Proc. Acad. Nat. Sci. Philadelphia. 435–444.
1912. Cell size and nuclear size. Journ. Exp. Zool. 12: 1–98.
1912a. Body size and cell size. Journ. Morph. 23: 159–188.
Donaldson, H. H.
1895. The growth of the brain. London and New York.
Driesch, H.
1898. Von der Beendigung morphogener Elementarprocesse. Arch. Entw.-Mech. 6: 198–227.
1900. Die isolirten Blastomeren des Echinidenkeimes. Arch. Entw.-Mech. 10: 361–410.
Engler, A. and Gilg. E.
1912. Syllabus der Pflanzenfamilien. Berlin.
Ewart, A. J.
1906. The influence of correlation upon the size of leaves. Ann. Bot. 20: 79–82.
Frank, A. B.
1895. Die Krankheiten der Pflanzen. 2 Aufl. 1: 271–277. Breslau.

Gates, R. R.
1909. The stature and chromosomes of Oenothera gigas, De Vries. Arch. Zellforsch. 3: 525–552.

Gauchery, P.
1899. Recherches sur le nanisme végétal. Ann. Sci. Nat. Bot. 8e. 9: 61–156.

Gaule, J.
1889. Zahl und Vertheilung der markhaltigen Fasern im Froschrückenmark. Ablandl. Math. Phys. Cl. K. Sächs. Gesell. Wiss. 15: 739–780.

Gerassimow, J. J.
1902. Die Abhängigkeit der Grösse der Zelle von der Menge ihrer Kernmasse. Ztschr. Allg. Physiol. 1: 220–258.

Gerry, Eloise.
1915. Fiber measurement studies, length variations; where they occur and their relation to the strength and uses of wood. Abstract in Science N. S. 61: 179.

Gregory, R. P.
1911. Note on the histology of the giant and ordinary forms of Primula sinensis. Proc. Phil. Soc. Cambridge. 15: 239–246.

Haberlandt, G.
1882. Vergleichende Anatomie des assimilatorischen Gewebesystems der Pflanzen. Jahrb. Wiss. Bot. (Pringsheim). 13: 74–188.

Hardesty, I.
1902. Observations on the medulla spinalis of the elephant with some comparative studies of the intumescentia cervicalis and the neurones of the columna anterior. Journ. Compar. Neur. 12: 125–182.

Hartig, R.
1901. Holzuntersuchungen. Berlin.

Hertwig, R.
1903. Über Korrelation von Zell — und Kerngrösse und ihre Bedeutung für die geschlechtliche Differenzierung und die Teilung der Zelle. Biol. Centbl. 23: 49–62, 108–119.

Heumann, G.
1850. Mikroskopische Untersuchungen an hungernden und verhungerten Tauben. Referat aus Canstatt's Jahresber. Fortschr. Gesam. Med. allen Ländern. 1: 140. 1852.

Illing, G.

1905. Vergleichende histologische Untersuchungen über die Leber der Haussaugetiere. Anat. Anz. 26: 177–193.

Jakushkine, O. W. and Wawilow, N.

1912. An anatomical study of certain races of oats with respect to the question of the relation between the anatomical structure and physiological characters of plants. (Russian). Zhur. Opuitn. Agron. 13: 830–861.

Jennings, H. S.

1908. Heredity, variation and evolution in Protozoa. II. Heredity and variation of size and form in Paramecium, with studies of growth, environmental action and selection. Proc. Am. Phil. Soc. 47: 393–546.

Keeble, F.

1912. Gigantism in *Primula sinensis*. Jour. Genetics. 2: 163–188.

Kolkunow, W. W.

1905. Development of drought resistant races of cereals. I. Anatomical-physiological investigations of the degree of drought resistance of certain cereals. (Russian.) Izv. Kiev. Politek. Inst. 5: No. 4; I–VIII and 1–82.

1907. Development of drought resistant races of plants. II. Anatomical-physiological investigations of the degree of drought resistance of some races of beets. (Russian.) Izv. Kiev. Politek. Inst. 7: No. 1; 1–76.

1907a. The relation between the size of the stomata and photosynthesis in grasses. (Russian). Zhur. Opuitn. Agron. 8: 369–381.

1913. The reciprocal relations between anatomical coefficients and physiological characters of plants. (Russian.) Zhur. Opuitn. Agron. 14: 321–340.

Kraus, G.

1869–70. Ueber die Ursachen der Formänderungen etiolirender Pflanzen. Jahrb. Wiss. Bot. (Pringsheim). 7: 209–260.

Lee, H. N. and Smith, E. M.

1916. Douglas fir fiber with special reference to length. Forestry Quart. 14: 671–695.

Levi, G.

1906. Studi sulla grandezza delle cellula. I. Recerche comparative sulla grandezza della cellule dei Mammiferi. Arch. Ital. Anat. Embriol. 5: 291–358.

Lippold, E.

1904. Pflanzenwelt Unterfrankens. III. Anpassung der Zwergpflanzen des Würzburgen Wellenkalkes nach Blattgrösse und Spaltöffungen. Verhandl. Phys. Med. Gesell. Würzburg. N. F. 36: 337–383.

MacCallum, J. B.

1898. On the histogenesis of the striated muscle fibre, and growth of the human sartorius muscle. Bull. Johns Hopkins Hospital. 9: 208–215.

Mohl, H. von.

1851. Grundzuge der Anatomie und Physiologie der Vegetabilischen Zelle. Braunschweig.

Morgan, T. H.

1904. The relation between normal and abnormal development of the embryo of the frog (III) as determined by some abnormal forms of development. Arch. Entw.-Mech. 18: 507–534.

Morgulis, S.

1911. Studies of inanition in its bearing upon the problem of growth. Arch. Entw.-Mech. 32: 169–268.

Morpurgo, B.

1888. Sul processo fisiologico di neoformazione celluare durante la inanizione acuta del'organisno. Arch. Sci. Med. 12: 395–419.

1889. Sur la nature des atrophies par inanition. Arch. Ital. Biol. 12: 333–338.

Paulmann, R.

1915. Über die Anatomie des Laubblattes. Flora. 107: 227–258.

Popoff, M.

1908. Experimentelle Zellstudien. Arch. Zellforsch. 1: 245–379.

Rabl, C.

1899. Über den Bau und die Entwicklung der Linse III. Ztschr. Wiss. Zool. 67: 1–138.

Sachs, J.

1893. Physiologische Notizen. VI. Über einige Beziehungen der specifischen Grösse der Pflanzen zu ihren Organisation. Flora. 77: 49–81.

Sanio, K.

1872. Über die Grösse der Holzzellen bei der gemeinen Kiefer (*Pinus silvestris*). Jahrb. Wiss. Bot. (Pringsheim). 8: 401–420.

1873–74. Anatomie der gemeinen Kiefer (*Pinus silvestris L.*) II. Jahrb. Wiss. Bot. (Pringsheim). 9: 50–126.

Schnegg, H.

1902. Beiträge zur Kenntnis der Gattung Gunnera. Flora. 90: 161–208.

Schramm, R.

1912. Über die anatomischen Jugendformen der Blätter einheimischer Holzpflanzen. Flora. 104: 225–295.

Schultz, E.

1904. Über Reductionen. I. Über Hungererscheinungen bei Planaria lactea L. Arch. Entw.-Mech. 18: 555–577.

Shepard, H. B. and Bailey, I. W.

1914. Some observations on the variation in length of coniferous fibers. Proc. Soc. Am. Foresters. 9: 522–527.

Sierp, H.

1914. Über die Beziehungen zwischen Individuengrösse, Organgrösse und Zellengrösse, mit besonderer Berücksichtigung des erblichen Zwergwuchses. Jahrb. Wiss. Bot. (Pringsheim). 53: 55–124.

Strasburger, E.

1893. Histologische Beiträge. 5. Über die Wirkungssphäre der Kerne und die Zellgrösse. 97–124. Jena.

Stoppenbrink, F.

1905. Der Einfluss herabgesetzter Ernährung auf den histologischen Bau der Süsswassertricladen. Zeit. Wiss. Zool. 79: 496–547.

Tenopyr, L. A.

1918. On the constancy of cell shape in leaves of varying shape. Bull. Tor. Bot. Club. 45: 51–77.

Tupper, W. W. and Bartlett, H. H.

1916. A comparison of the wood structure of *Oenothera stenomeres* and its tetraploid mutation *gigas*. Genetics 1: 177–184.

1918. The relation of mutation characters to cell size. Genetics. 3: 93–106.

Williamson, W. C.

1871. On the organization of the fossil plants of the Coal-Measures. I. Calamites. Phil. Trans. Roy. Soc. London. 161: 477–510.

1873. On the organization of the fossil plants of the Coal-Measures. IV. Dictyoxylon, Lyginodendron, and Heter-

angium. Phil. Trans. Roy. Soc. London. 163: 377–408.

Williamson, W. C. and Scott, D. H.

1894. Further observations on the organization of the fossil plants of the Coal-Measures. I. Calamites, Calomostachys and Sphenophyllum. Phil. Trans. Roy. Soc. London. 185: 863–960.

1895. Further observations on the organization of the fossil plants of the Coal-Measures. III. Lyginodendron and Heterangium. 186: 703–780.

Winkler, H.

1916. Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. Zeit. Bot. 8: 417–531.

Yapp, R. H.

1912. *Spiraea ulmaria* L. and its bearing on the problem of xeromorphy in marsh plants. Ann. Bot. 26: 815–870.

Zalenski, W.

1904. Quantitative anatomy of different leaves of the same plants. (Russian.) Izv. Kiev. Politek. Inst. 4: No. 1; 1–208.